A STUDY OF THE ECTOPARASITES OF ALCIDS IN NEWFOUNDLAND

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A STUDY OF THE ECTOPARASITES OF ALCIDS IN NEWFOUNDLAND

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ABSTRACT

Three groups of ectoparasites, namely, Mallophaga, ticks and feathermites, were recovered from two hundred and sixty-seven alcids of six species (*Alca torda, Uria aalge, Uria lomvia, Plautus alle, Cepphus grylle, Fratercula arctica*) examined. Mallophaga of the genera *Saemundssonia, Quadraceps* (Ischnocera) and *Austromenopon* (Amblycera) were recovered from five alcids; only *Saemundssonia* and *Quadraceps* from *C. grylle*. One species of ixodid tick, *Ixodes (Ceratitodes) uriae*, was recovered from all but *P. alle* and *C. grylle*; the majority of which were examined in the winter. Only *A. torda* and *F. arctica* harboured feathermites belonging to the genus *Alloptes*. Four new geographical records and one new host record are reported.

No significant difference ($P > 0.05$) was found in the mallophagan infestation of hosts and in the tick infestation of *U. aalge* from year to year. The tick infestation of *F. arctica* differed in 1972 and 1973, probably due to few immature *Larus argentatus* being present in the colony during the latter year. No significant difference was noted for the mallophagan and tick infestation of hosts with regard to sex of the hosts. A correlation was noted only between the weight and mallophagan infestation of *U. lomvia*.

Data on the degree of infestation of both adults and chicks with each parasite species are presented. The infestation of adult hosts was related to the host habitat. Chicks were always more heavily infested with Mallophaga than adults. Fluctuations, related to the host biology, occurred in the mallophagan population on *F. arctica*. Details on the transfer of Mallophaga from adults to chicks are given.

The distribution of each parasite species on the hosts was determined; the same mallophagan genus generally occupying the same habitat on the different host species. The tick distribution on hosts varied with the host species.

The population dynamics of each mallophagan species on each alcid was examined. Due to increased reproductive activity, nymphs were more common on adults during the winter and were always dominant on chicks. The sex ratio of each species varied with the host, females being generally more common in winter and on chicks. Correlations were determined for the stages and sexes of each species population on hosts.

An ischnoceran and an amblyceran occupied virtually the same habitat on the hosts with correlations always existing between them. No interspecific competition existed between the genera on each host. All stages and sexes of the total mallophagan population on hosts were correlated.

Ixodes ariae preferred *U. aalge* as hosts. Their

distribution in the colony was affected by the density of the hosts and the substrate. The seasonal activity of the tick in the hesting areas and on the hosts were similar. The engorgement time for each stage on various hosts was determined and their percentage increases in weight recorded. The pathological reaction of the host's skin to tick attachment is described. Observations were made on reproduction and measurements made of a spermatophore. The oviposition rate and the development of each stage under different temperatures and humidity regimes was determined. The life-cycle, based on field and laboratory data, is presented.

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PART I

GENERAL SURVEY OF ECTOPARASITES

Introduction

The alcids (Charadriiformes: Alcidae) are a holoartic group of essentially pelagic seabirds breeding around the fringes of the Arctic Ocean (Austin, 1961). Members of this group tend to congregate in colonies during nesting throughout their range (Demet'ev and Gladkov, 1951; Kozlova, 1957). Certain coastal islands and inlets in Newfoundland are breeding grounds for five species of alcids namely, the Razorbill (*Alca torda* L.), the Common Murre (*Uria aalge* (Pont.)), the Thick-billed Murre (*Uria lomvia* (L.)), the Black Guillemot (*Cepphus grylle* (L.)) and the Common Puffin (*Fratercula arctica* (L.)), the major colonies being at Witless Bay and Funk Island (Tuck, 1960). A sixth species, the dovekie (*Plautus alle* (L.)), an arctic breeder, occurs along the coast in winter (Demet'ev and Gladkov, 1951; Godfrey, 1966).

Although many aspects of the biology of certain species of these birds, such as the Common Puffin (Lockley, 1953; Nettleship, 1972) and the murres (Tuck, 1960) have been studied, little attention has been given to their ecto-parasite fauna. Markov (1937) noted changes in the mallophagan

fauna, related to age, of the Thick-billed Murre in Novaya Zemlya, U.S.S.R. Belopolskaya (1947; *vide* Uspenskii, 1956) reported that Common Murres in Seven Islands, on the East Murman coast, were more heavily infested than Thick-billed Murres, being parasitized by six species of ecto-parasites. The same author (Belopolskaya, 1952) noted the degree of infestation with mallophagans, ticks and feather-mites of Razorbills, Common Murres, Thick-billed Murres, Black Guillemots and Common Puffins in the U.S.S.R. Flint and Kostyrke (1967) worked on the biology of the seabird tick *Ixodes (Ceratixodes) uriae* White, 1842 noting that, of the birds inhabiting colonies on the northeastern shore of Murman, the preferred host was the Common Murre. Karpovich (1970) reported similar results in a more detailed study of this tick infesting seabirds on islands in East Murman. The majority of other works published on this subject are concerned merely with records of occurrence in nature, or taxonomy.

In view of this apparent lack of published material on the ectoparasites of alcids, a study was initiated in 1972 to examine various aspects of the ectoparasite fauna of the six species of alcids occurring in Newfoundland. The main aim of this study was to obtain data on the biology of any organisms recovered; including their frequency of occurrence within the host population, the degree of host infestation, their distribution on the host, their population

dynamics, and, where possible, their life-cycle. The examination of chicks and adults of certain host species during the breeding season provided phenological data on adult-to-chick transfer of Mallophaga, the effect of this transfer on the population dynamics of the Mallophaga on adult birds, and changes in the ectoparasite fauna with increasing age of the host. The effect of host habitat on the ectoparasites was also examined.

Threlfall (1968) noted that Herring Gull (*Larus argentatus* Pont.) chicks in the Witless Bay Seabird Sanctuary were infested with *Ixodes uriae*, Main (1973) reporting two new arboviruses from this tick in the same area. In spite of its potential as a vector of viruses to seabird and human populations, little work has been done on its bionomics. An attempt was made, through field and laboratory studies, to obtain data on various aspects of its feeding, its host preferences, the host reaction to its attachment, its reproduction, development and life-cycle.

It is hoped that this work will provide much needed basic data on the biology of these ectoparasites of alcids. As the work progressed, it became increasingly evident that two distinct studies were developing; one being a general survey of the ectoparasites and the other a study of the biology of the tick, *Ixodes uriae*. For this reason, it was decided to treat these studies separately.

MATERIALS AND METHODS

The birds examined in the present study (Table 1) were collected in two main areas: The Witless Bay Seabird Sanctuary (WBSS--47° 15'N 52° 47'W) and Hillgrade, New World Island, Notre Dame Bay (NDB--49° 32'N 54° 47'W) (Fig. 1) using a variety of trapping techniques and by shooting.

Most of the birds were euthanased upon capture and, like those shot, placed in individual plastic bags to prevent ectoparasite migration between hosts, labelled, and frozen for future examination.

To determine the distribution of the ectoparasites on hosts, the body was abritrarily divided into 12 regions (Fig. 2).

A number of birds were examined for ectoparasites in the field. These birds were placed in a large, transparent-glass bottle equipped with a stopper on which was fastened several gauze pads moistened with ether. After several minutes, or when the bird was sedated, it was removed and examined for ectoparasites by deflecting the feathers with forceps and removing any organisms seen. The bird was then weighed (OHAUS, Model 8014) measured (according to Godfrey, 1966), banded and released. This method proved to be effective in that it immobilized the parasites, making their

TABLE 1

DETAILS ON SPECIES OF BIRDS EXAMINED DURING THE STUDY

Species	No.* & Age	Locality	Date Caught	Method of Capture
Razorbill (*Alca torda* L.)	3 Chicks; 1 Adult	W.B.S.S.	July, 1972	By hand
	1 Adult	N.D.B.	December, 1972	Shot
	1 Chick; 2 Adults	W.B.S.S.	July, 1973	By hand
Common Murre (*Uria aalge* (Pont.))	6 Chicks;12 Adults	W.B.S.S.	July, 1972	By hand; Salmon dip-net
	1 Adult	N.D.B.	December, 1972	Shot
	16 Adults	W.B.S.S.	July, 1973	Noose pole
Thick-billed Murre (*Uria lomvia* (L.))	32 Adults	N.D.B.	November, 1972	Shot
	20 Adults	N.D.B.	December, 1972	Shot
	2 Chicks; 1 Adult	W.B.S.S.	July, 1973	Salmon dip-net
Dovekie (*Plautus alle* (L.))	1 Adult	N.D.B.	November, 1972	Shot
	17 Adults	N.D.B.	December, 1972	Shot
Black Guillemot (*Cepphus grylle* (L.))	2 Adults	N.D.B.	November, 1972	Shot
	8 Adults	N.D.B.	December, 1972	Shot
Common Puffin (*Fratercula arctica* (L.))	7 Adults	W.B.S.S.	May, 1972	20 fathom herring net
	2 Adults	W.B.S.S.	June, 1972	20 fathom herring net
	1 Chick; 11 Adults	W.B.S.S.	July, 1972	By hand; shot
	5 Chicks;10 Adults	W.B.S.S.	August, 1972	By hand; 20 fathom herring net
	6 Chicks; 6 Adults	W.B.S.S.	September, 1972	By hand; shot
	2 Adults	N.D.B.	December, 1972	Shot
	7 Adults	W.B.S.S.	May, 1973	20 fathom herring net
	14 Adults	W.B.S.S.	June, 1973	20 fathom herring net
	18 Adults	W.B.S.S.	July, 1973	20 fathom herring net
	3 Chicks; 2 Adults	W.B.S.S.	August, 1973	By hand; shot

*Does not include birds examined and released.

FIGURE 1

Sampling areas:

1. Witless Bay Seabird Sanctuary (WBSS).
2. Hillgrade, Notre Dame Bay (NDB).

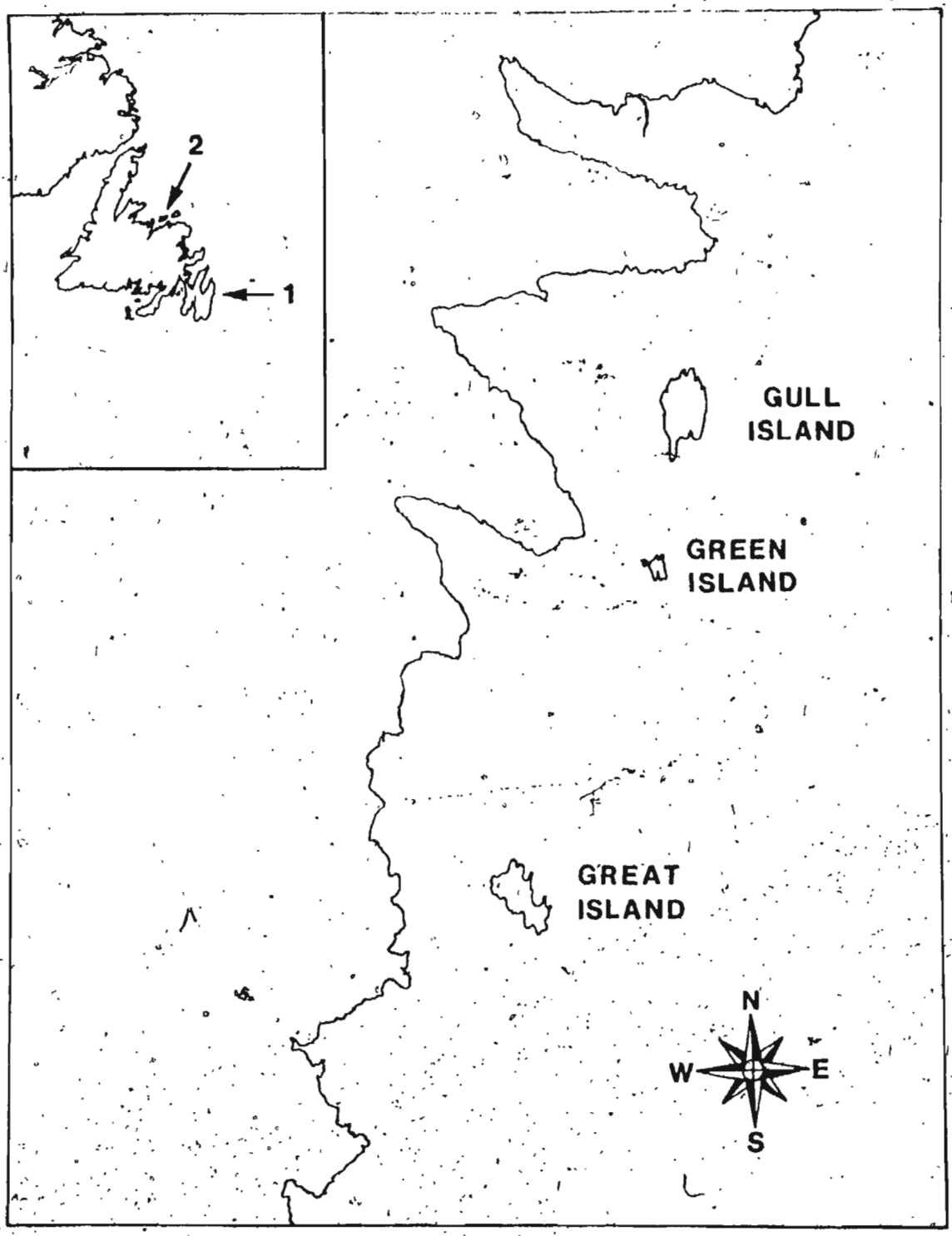
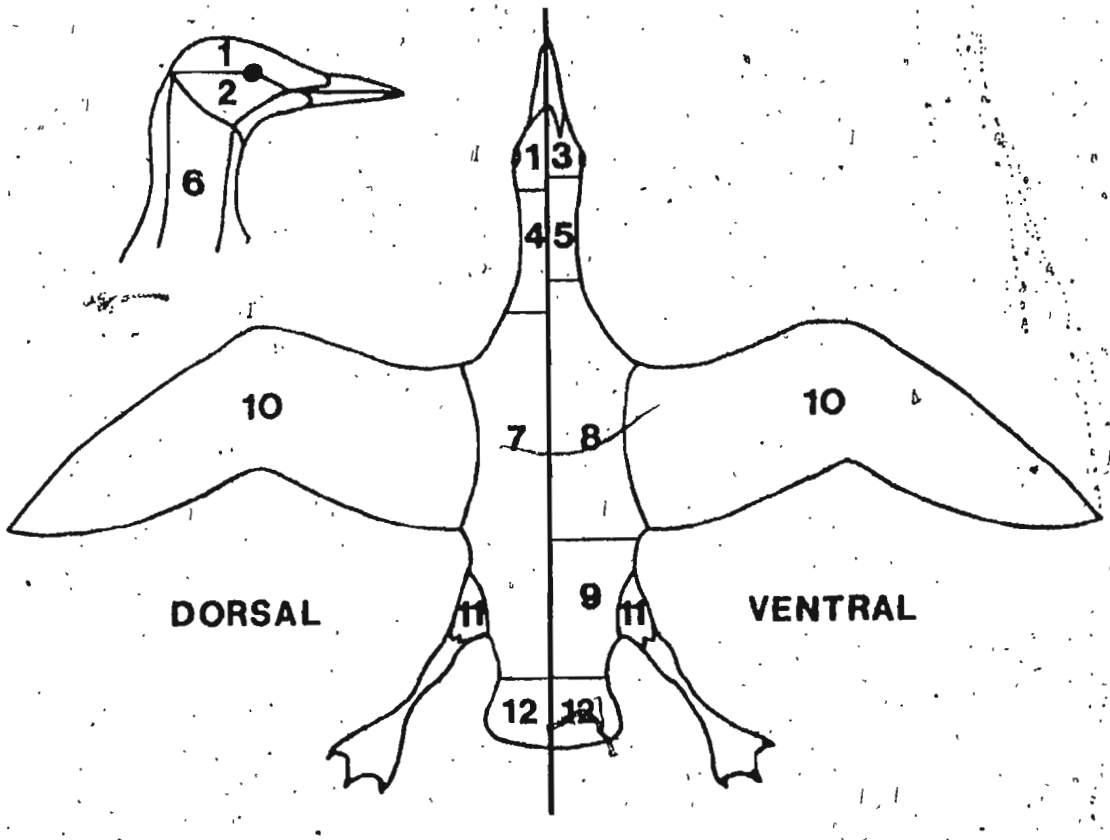

2
1
GULL
ISLAND
GREEN
ISLAND
GREAT
ISLAND
N
W
E
S

FIGURE 2

Body regions of hosts.

1 CROWN
2 AURICULAR
3 GULAR
4 NAPE
5 JUGULUM
6 SIDE OF NECK

7 BACK
8 BREAST
9 ABDOMEN
10 WINGS
11 LEGS
12 TAIL



removal easier and it also allowed examination of all body regions.

Birds that were examined in the laboratory were placed in a white enamel dish (39 cm. x 31 cm.) under an overhead fluorescent lamp equipped with a 12 cm. diameter magnifying lens. Forceps were used to deflect the feathers, exposing the ectoparasites. Each region was examined individually and any ectoparasites seen were removed and placed in 70% alcohol, their location being recorded. The birds were weighed, measured and sexed after examination to avoid accidental loss of ectoparasites during handling. At a later date the ectoparasites were separated on the basis of species, sex and stage of development and counted. The results were analysed using standard statistical methods. Permanent mounts were made of representatives of each species of ectoparasite recovered using Rubin's fluid (Rubin, 1951).

Using the above method, few Mallophaga, probably less than 5 percent, would be missed. All birds were examined in the same manner thus figures are comparable.

RESULTS AND DISCUSSION

Three groups of ectoparasites namely, Mallophaga, ticks and feathermites were recovered from the alcids examined.

I. Mallophaga

Adults and nymphs of *Saemundssonia* spp., *Quadraceps* spp. (Ischnocera: Philopteridae) and *Austromenopon* spp. (Amblycera: Menoponidae), representing two suborders and two families were recovered from the 267 alcids of 6 species examined. Specimens of *Saemundssonia* and *Quadraceps* were recovered from all species of alcids examined; *Austromenopon* from all except *Cepphus grylle*. A search of the literature revealed that, to date, no *Austromenopon* spp. have been recorded from the latter host. Taxonomic designations follow the works of Clay (1959), Emerson (1972) and Timmerman (1949, 1954a, b; 1957, 1963, in litt.).

II. Ticks

Parasitic stages of one species of ixodid tick, *Ixodes (Ceratixodes) uriae* White, 1852, were recovered from 41 alcids of 4 of the 6 species examined. No specimens were recovered from *Plautus alle* and *Cepphus grylle* as most of these hosts were examined after the breeding season.

III. Feathermites

Specimens of one genus of feathermites, *Alloptes* were recovered from 4 alcids of 2 of the 6 species examined, namely *Alca torda* and *Fratercula arctica*.

The ectoparasites recovered will be discussed under each host species. All measurements are given in microns (μ) unless otherwise stated.

A. Common Puffin (*Fratercula arctica* (L.))

Specimens of *Saemundssonia fraterculae* (Overgaard, 1942), *Quadraceps helgovauki* Timmerman (in litt.) and *Austromenopon nigropleurum* (Denny, 1842) were recovered from *F. arctica*. Details of the infestation of *F. arctica* are given in Table 2 and the frequency distribution in Fig. 3. The distribution is of the "hollow curve" type described by Williams (1964) in which the majority of the hosts have a few parasites, and the majority of the parasites are on a few hosts.

No significant difference ($P > 0.05$) was found between the mallophagan populations in 1972 and 1973 nor were significant differences ($P > 0.05$) found in the mallophagan burden of adult *F. arctica* with regard to sex and weight of the host.

Although Mallophaga live in a relatively constant environment amongst the hosts' feathers, monthly fluctuations occurred in the population (Table 3). The average infestation

TABLE 2

DETAILS ON THE INFESTATION OF ADULTS AND CHICKS OF *FRATERCULA ARCTICA* WITH MALLOPHAGA

Age	No. examined	Percent infested	Mean	Range
Adult	125*	67.2	7.3	1 - 56
Chick	15	80.0	35.0	2 - 135

* 2 specimens from N.D.B. not included.

FIGURE 3

Frequency distribution of Mallophaga on adult *Fratercula arctica*.

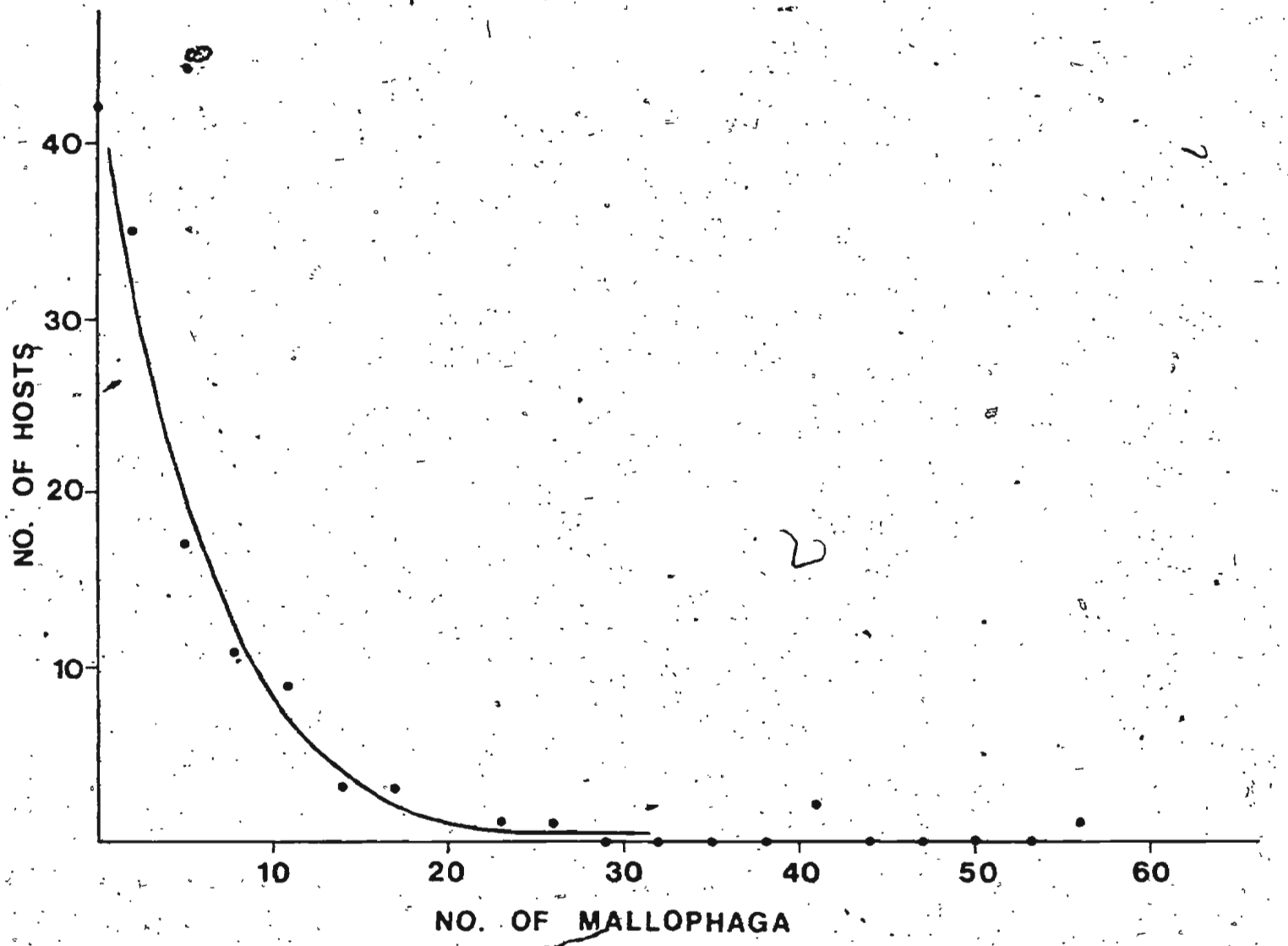

NO. OF HOSTS
40
30
20
10
10
20
30
40
50
60
NO. OF MALLOPHAGA

TABLE 3

MONTHLY INFESTATION OF ADULTS AND CHICKS OF *FRATERCULA ARCTICA* WITH MALLOPHAGA DURING 1972 AND 1973

Month	May		June		July		August		September	
Age	Adult	Chick	Adult	Chick	Adult	Chick	Adult	Chick	Adult	Chick
No. Hosts Examined	31	-	47	-	29	1	12	8	6	6
% Infested	74.2	-	57.4	-	62.1	100	92.5	75	83.3	83.3
No. Mallophaga	149	-	204	-	135	37	47	162	79	222
Mean	6.5	-	7.6	-	7.5	37	4.3	27	15.8	44.4
Range	1-18	-	1-56	-	1-41	37	1-11	3-135	3-42	2-127

increased in June, decreased slightly in July and reached a minimum in August. In September the infestation sharply increased again.

The high infestation in May and the peak in June could be attributed to increased nesting activity (Woodman and Dicke, 1954; Ash, 1960; Touleshkov, 1965) when opportunities for transfer are optimum, or another possibility could be that reported by Foster (1969) for the Mallophaga of the Orange-crowned Warbler (*Vermivora celata*). She found that the maximum breeding period of Mallophaga is timed so that maximum population numbers occur prior to the hatching of the host's eggs. *F. arctica* chicks start hatching in July (Bradley, 1971) at which time the infestation on adult hosts began to decrease. In August maximum transfer from adults-to-chicks occurred since the majority of chicks have hatched and some are near fledging age. The high infestation in September may be the result of an increase in breeding activity by Mallophaga to ensure survival during the host postnuptial molt. One also cannot discount the possibility that chick-to-adult transfer occurs, especially in September when numbers of Mallophaga on chicks are maximum (Table 3). In the field and laboratory, Mallophaga on chicks will readily transfer* on handling, therefore, chick-to-adult transfer is possible and could help to account for the increase in infestation of adults at the peak of chick infestation. These results are similar

*From bird to examiner.

to those of Touleshkov (1965) who worked on starlings (*Sturnus vulgaris* L.).

While it is difficult to account for such large numbers per infested chick (Table 3), there is little doubt that breeding must occur on the chicks since such large numbers were very rarely recovered from adult hosts. Although careful scrutiny of wild chicks revealed no eggs, the only eggs that were recovered during the present work were taken from laboratory-reared chicks. Furthermore, the majority of specimens recovered from chicks were nymphs (1.71 nymphs per adult on chicks as opposed to only 0.40 nymphs per adult on adult hosts).

The exact time of transfer from adults-to-chicks could not be accurately established but, one chick taken approximately 1-2 days after hatching (53 gm.), harboured Mallophaga. Markov (1937) reported that Mallophaga occurred on *U. lomvia lomvia* as early as the first to the fifth day after hatching in Novaya Zemlya, U.S.S.R. Van Den Broek (1967) also reported Mallophaga on chicks of the Black-headed Gull (*Larus ridibundus*) only several hours old.

In the present study it was found that specimens of *Quadraceps helgovauki* were the first to transfer, being the only species found on chicks between 53 gms. and 191 gms. in weight (assuming that weight is some indication of age). Chicks between 192 and 301 gms. in weight harboured *Saemundssonia fratercula* and it appeared that the numbers of

this species were becoming more prominent, increasing from 0 to 9.2 specimens per infested chick, while *Quadraceps helgovauki* decreased from 45.8 specimens to 22.7 specimens per infested chick. The only exception was one chick weighing 218 gms., its entire population being *Quadraceps helgovauki*. Markov (1937) noted that on *U. lomvia lomvia*, *Nirmus obliquus* occurred only on chicks more than 15 or 20 days old. It is also interesting to note that *Quadraceps helgovauki* is not the dominant species on adult *F. arctica*.

Saemundssonia fratercula (Overgaard, 1942)

This is a rather short, stout ischnoceran found mainly on the feathers of the head and neck of its hosts. The adults were generally found resting on the ventral surface of the feathers with their mouthparts "wrapped round" the barbules, sometimes making their removal difficult. Many specimens were found with their bodies parallel to the barbs and their heads directed towards the shaft of the feathers as noted by Stenram (1956). The nymphs, however, were rarely found attached to feathers and upon disturbance of the feathers could be seen running towards the base of the feathers and over the skin of the host. The presence of pieces of feathers in the crops of many specimens indicate that it is a feather feeder.

S. fratercula has previously been reported from *F. arctica* in Europe (Timmerman, 1957), Iceland (Overgaard,

1942) and North America (Emerson, 1972). In the present study it was the most common parasite on adult *F. arctica*, being found on 96.4% of the infested birds and the only species on 79.4% of those birds. The frequency distribution of *S. fratercula* (Fig. 4) is very similar to that of the total population (Fig. 3), indicating the dominance of this species on adult hosts. The mean number per infested host was 5.4 (range 1-25) lice.

All stages (except eggs) were found on the hosts examined. Table 4 details the distribution of the stages and sexes found on the hosts examined. It is evident that this species is accurately termed a "head" louse as 98.1% were recovered from the head and neck regions of adult hosts. On the head, 40.1% occupied the gular region, 16.1% the auricular region and only 4.2% from the crown region. On the neck, 21.4% were recovered from the jugulum, 8.5% and 7.8% from the nape and sides of the neck, respectively. It is interesting to note that 61.8% of the specimens were recovered from the ventral regions of the head and neck. The majority (63.2%) of the specimens recovered from the crown were nymphs, probably indicating that this may be the site of oviposition or an area in which to avoid preening by the host.

The population structure of *S. fratercula* in relation to the total population on adult *F. arctica* is given in Fig. 5. The numbers of males and females follow similar

FIGURE 4

Frequency distribution of each mallophagan species on adult *Fratercula arctica*.

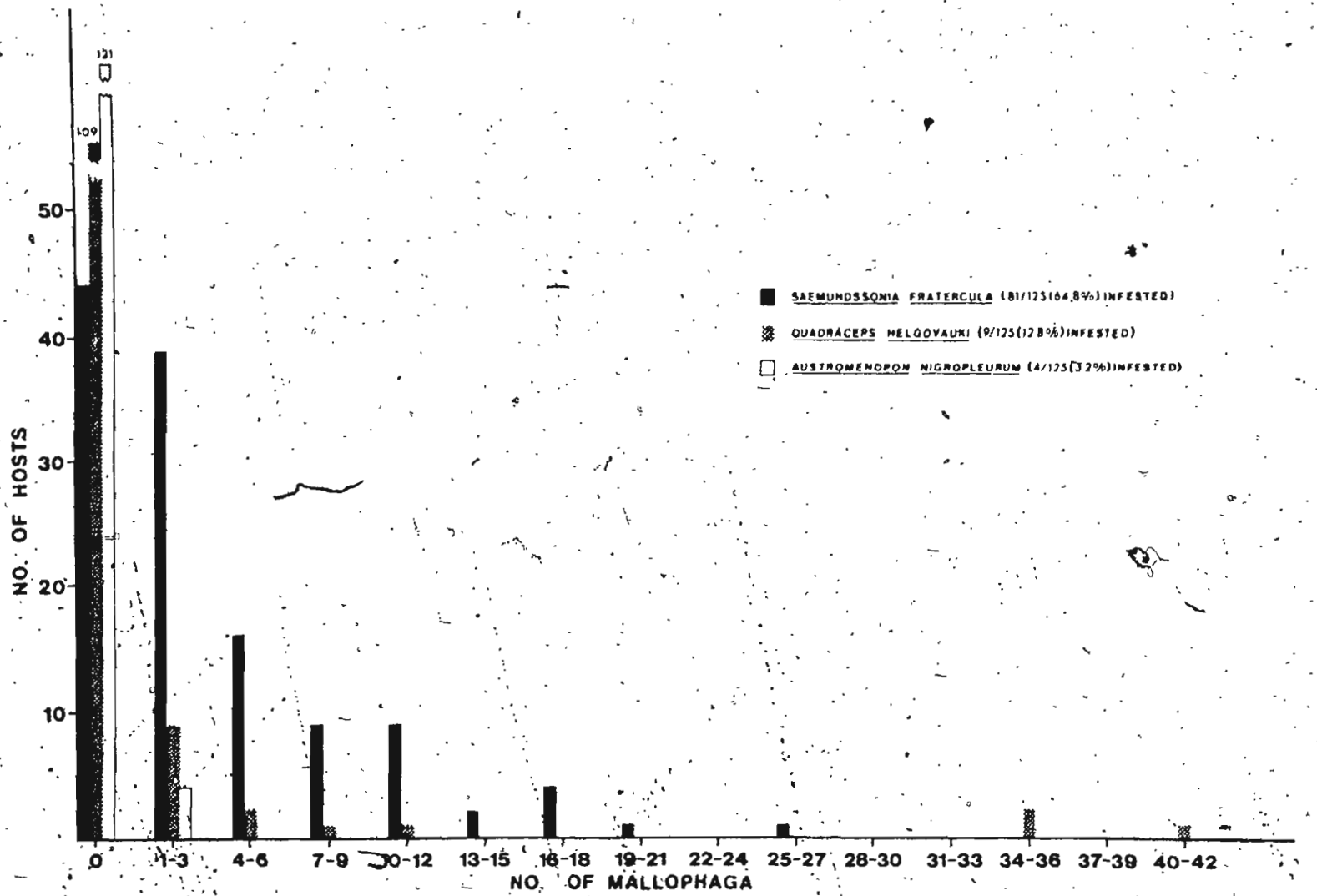

NO. OF HOSTS
50
40
30
20
10
0
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
28-30
31-33
34-36
37-39
40-42
NO. OF MALLOPHAGA
SAEMUNDSSONIA FRATERCULA (81/125(64,8%) INFESTED)
QUADRACEPS HELGOVAUKI (9/125(12,8%) INFESTED)
AUSTROMENOPON NIGROPLEURUM (4/125(3,2%) INFESTED)

TABLE 4

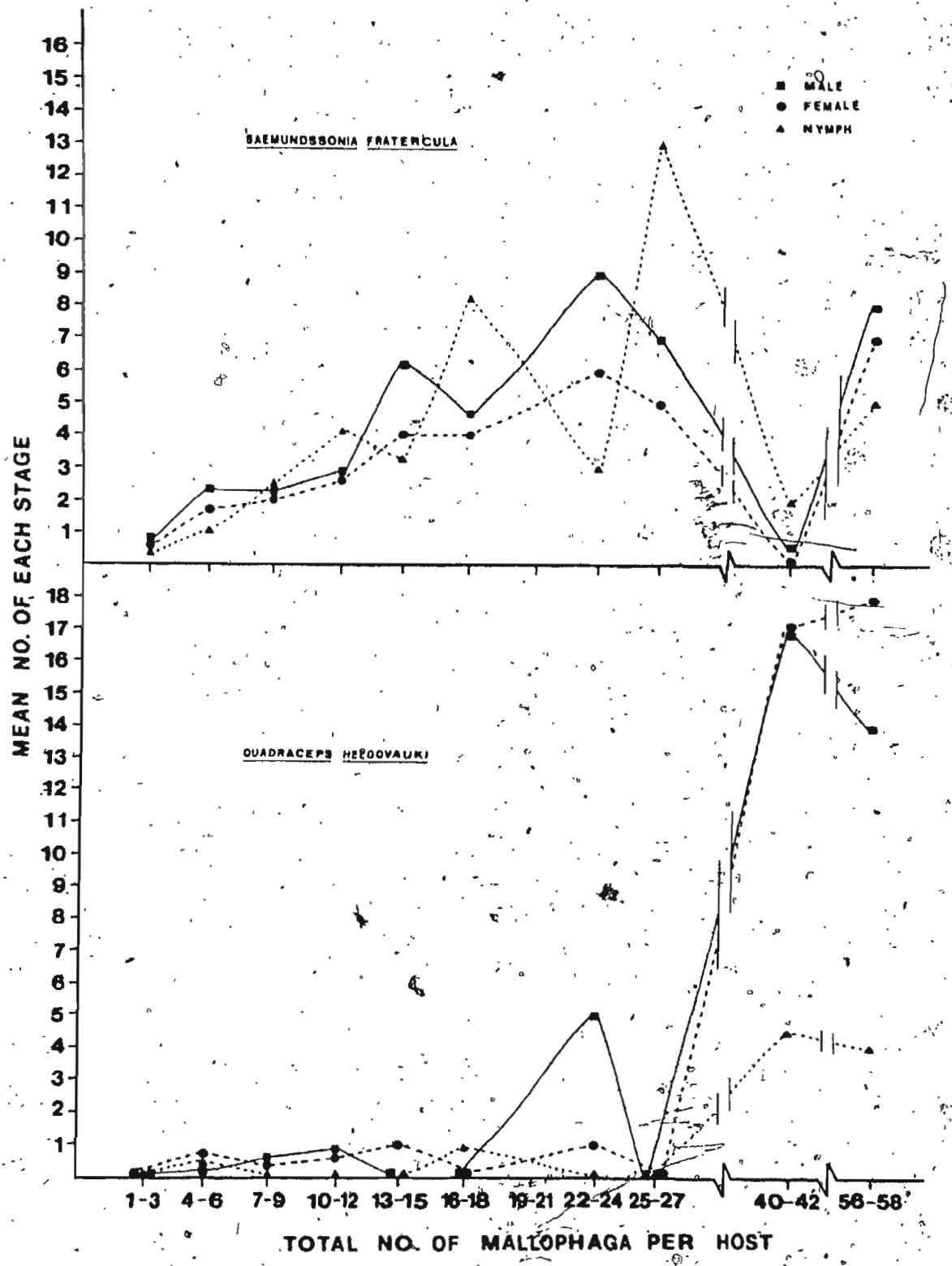
DISTRIBUTION OF *SAEMUNDSSONIA FRATERCULA* ON ADULT *FRATERCULA ARCTICA**

Stage		Crown	Auricular	Gular	Jugulum	Nape	Side of neck	Back	Breast
Nymph	No. hosts infested	6	20	20	18	7	9	2	2
	% Total infested.	12.2	40.8	40.8	36.7	14.3	18.4	4.1	4.1
	Total No. in region.	12	37	50	21	14	17	5	3
	Mean.	2	1.9	2.5	1.2	2	1.9	2.5	1.5
	Range.	1-3	1-8	1-7	1-2	1-5	1-6	1-4	1-2
	% Total *Mallophaga* in region.	63.2	50.7	27.5	21.6	36.8	48.6	62.5	100
Male	No. hosts infested	3	14	32	22	8	9	2	0
	% Total infested.	4.5	6.1	48.5	33.3	12.1	13.6	3	0
	Total No. in region.	3	24	69	42	17	9	3	0
	Mean.	1	1.6	2.2	1.9	2.1	1	1.5	0
	Range.	1	1-4	1-9	1-5	1-6	1	1-2	0
	% Total *Mallophaga* in region.	15.7	31.5	38	43.3	44.7	25.7	37.5	0
Female	No. hosts infested	2	9	32	19	5	7	0	0
	% Total infested.	3.6	16.4	58.2	34.5	9.1	12.7	0	0
	Total No. in region.	4	13	63	34	7	9	0	0
	Mean.	2	1.4	2	1.8	1.4	1.3	0	0
	Range.	1-3	1-2	1-8	1-7	1-3	1-2	0	0
	% Total *Mallophaga* in region.	21.1	17.8	34.5	35.1	18.5	25.7	0	0
Total	No. hosts infested	8	31	49	32	11	17	3	2
	Total No. in region	19	74	182	97	38	35	8	3
	Mean.	2.4	2.4	3.7	3.0	3.5	2.1	2.7	1.5
	Range.	1-4	1-8	1-18	1-14	1-14	1-6	1-4	1-2
	% Total recovered	4.2	16.1	40.1	21.4	8.5	7.8	1.8	0.1

*No specimens were recovered from the abdomen, wings, legs and tail.

FIGURE 5

The population structure of each mallophagan species in relation to the total population on adult *Fratercula arctica*.


MALE
FEMALE
NYMPH
SAEMUNDSSONIA FRATERCULA
QUADRACEPS HEPPOVAUKI
MEAN NO. OF EACH STAGE
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
40-42
56-58
TOTAL NO. OF MALLOPHAGA PER HOST

patterns throughout the population and were found to exhibit a high degree of relationship ($r = 0.58^{***}$, $df = 73$). When one considers the disparity found between the sexes on some hosts, this correlation is surprising. Buxton (1941) reported similar results in studies on populations of the human head-louse (*Pediculus humanis capitis*; Anoplura) which also exhibited erratic ratios on some hosts. Nymphs appeared to fluctuate and showed no correlation with either males or females ($r = 0.16$ (N.C.), $df = 70$ and $r = 0.06$ (N.C.), $df = 68$ respectively). A relationship did exist, however, between the numbers of adults and nymphs ($r = 0.27^{*}$, $df = 77$). One would think that the number of nymphs would be dependent, especially on the number of females as reported by Buxton (1941) for the human head-louse. In this case, it appears that both sexes must act together on the nymph population. Only 34.8% of the population were nymphs probably indicating that adults have low mortality or low reproductive rates. The sex ratio was 1:0.81 (160 m : 130 f).

Saemundssonia fratercula was not the dominant species on *F. arctica* chicks (as it was on adults), being found on only 50% of the infested hosts. Only one chick harboured this species as its sole mallophagan. The average number per infested chick was 4.7 (range 1 - 27) lice.

As on adult hosts, the majority of specimens (98.2%) were recovered from the head and neck regions (Table 5).

*** highly significant
* significant

TABLE 5

DISTRIBUTION OF *SAEMUNDSSONIA FRATERCULA* ON *FRATERCULA ARCTICA* CHICKS*

Stage		Crown	Auricular	Gular	Jugulum	Nape	Side of neck	wing
Nymph	No. hosts infested.	2	2	1	2	2	2	1
	% Total infested.	40	40	20	40	40	40	20
	Total No. in region	3	14	1	2	2	6	1
	Mean.	1.5	7	1	1	1	3	1
	Range.	1-2	2-12	1	1	1	2-4	1
	% Total *Mallophaga* in region.	30	58.4	100	50	33.3	60	100
Male	No. hosts infested.	1	3	0	0	2	1	0
	% Total infested.	25	75	0	0	50	25	0
	Total No. in region	4	5	0	0	3	2	0
	Mean.	4	1.7	0	0	1.5	2	0
	Range.	4	1-3	0	0	1-2	2	0
	% Total *Mallophaga* in region.	40	20.8	0	0	50	20	0
Female	No. hosts infested.	3	3	0	1	1	2	0
	% Total infested.	75	75	0	25	25	50	0
	Total No. in region	3	5	0	2	1	2	0
	Mean.	1	1.7	0	2	1	1	0
	Range.	1	1-3	0	2	1	1	0
	% Total *Mallophaga* in region.	30	20.8	0	50	16.7	20	0
Total	No. hosts infested.	3	4	1	2	3	2	1
	Total No. in region	10	24	1	4	6	10	1
	Mean.	3.3	6	1	2	2	5	1
	Range.	1-7	1-16	1	1-3	1-3	3-7	1
	% Total recovered.	17.8	42.9	1.8	7.1	10.7	17.9	1.8

*No specimens recovered from the breast, abdomen, back, legs and tail.

However, unlike the situation in adult hosts (Table 4), the majority of specimens (42.9%) were found on the auricular region and only 8.9% were recovered from the ventral regions of the head and neck. In contrast to adult hosts, nymphs were the dominant age class in most regions probably indicating increased reproductive activity on these hosts. The sex ratio was nearly 1 : 1 (14 m : 13 f).

In May and June the infestation of adult *F. arctica* was high, decreasing to a minimum in July (Table 6). In August the infestation climbed again reaching a maximum in September.

It is also interesting to note that the number of nymphs per infested host was highest in May and September. This supports the hypothesis of Foster (1969) that on the basis of what is known about the mallophagan life-cycle and its synchronization with that of the host, the nymphs will be most abundant in late spring, summer and early fall.

In July no specimens of *S. fratercula* were recovered from *F. arctica* chicks but this may be a reflection of the small sample size. As with adult hosts, the infestation reached a maximum in September, increasing by 40% over August. This is the time when the majority of chicks are ready to fledge. It may be postulated that if the numbers of *S. fratercula* continued to rise each month, it would become the dominant species by the following spring as on

TABLE 6

MONTHLY INFESTATION OF *FRATERCUBA ARCTICA* WITH *SAEMUNDSSONIA FRATERCULA*

	May		June		July		August		September	
	Adult	Chick	Adult	Chick	Adult	Chick	Adult	Chick	Adult	Chick
No. Hosts Examined	31	-	47	-	29	-	12	8	6	6
% Infested	74.2	-	57.4	-	55.2	-	83.3	25.0	83.3	66.7
Total No. of *S. fratercula*	149	-	162	-	65	-	43	3	37	53
Av. No. per infested host	6.5	-	6.0	-	4.1	-	4.3	1.5	7.4	13.3
Range	1-18	-	1-25	-	1-18	-	1-10	1-2	1-16	2-27
No. Males	38	-	72	-	27	-	15	1	15	13
No. Males per infested host	1.7	-	2.7	-	1.7	-	1.5	0.5	3.0	3.3
No. Females	33	-	51	-	21	-	18	1	7	12
No. Females per infested host	1.4	-	1.9	-	1.3	-	1.8	0.5	1.4	3.0
No. Nymphs	78	-	39	-	17	-	10	1	15	28
No. Nymphs per infested host	3.4	-	1.4	-	1.1	-	1.0	0.5	3.0	7.0

adult *F. arctica*.

Quadraceps helgovauki Timmermann (In litt.)

This is a rather long, slender ischnoceran recovered mainly from the back and breast of its hosts. It was generally found in the feathers in a similar position to that mentioned for *Saemundssonia fratercula* except that its slender body enables it to lie between the barbs of the feathers. This probably is an adaptation to avoid the preening of the host. Pieces of feathers removed from the crops of many specimens indicate that it is a feather-feeder.

This is the first record of *Q. helgovauki* from *F. arctica* in North America having only previously been recorded from this host in Europe (Timmermann (in litt.)). Measurements of specimens, as compared with those of Timmermann are given in Table 7. The frequency distribution (Fig. 4) is quite unlike that of *S. fratercula*, being found in small numbers on the majority of hosts. Only 19% of the infested adult hosts harboured this species with only two hosts having *Q. helgovauki* as their sole mallophagans. The average number per infested host was 1.9 (range 1-41) lice.

In contrast to adult hosts, *Q. helgovauki* was the dominant species on chicks, being recovered from 91.7% of the infested hosts examined (mean 30 per infested host (range 2-135)). Six chicks (50%) harboured only this species.

All stages (except eggs) were recovered from adult

TABLE 7

MEASUREMENTS (μ) OF MALE AND FEMALE *QUADRACEPS HELGOVOUKI* COMPARED WITH THOSE OF TIMMERMANN, IN LITT. (MM).

	Male								Female							
	Timmermann, in litt.				Present Study				Timmermann, in litt.				Present Study			
	Length		Width		Length		Width		Length		Width		Length		Width	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Head	0.49	0.48-0.50	0.37	0.36-0.38	475	452-499	368	358-384	0.53	0.49-0.54	0.40	0.38-0.41	493	442-525	394	353-416
Prothorax	-	-	-	-	127	120-150	255	249-270	-	-	-	-	129	120-140	264	234-280
Pterothorax	-	-	-	-	165	145-176	324	317-348	-	-	-	-	175	166-197	343	322-369
Abdomen	-	-	-	-	756	707-800	426	400-473	-	-	-	-	1039	930-1107	524	468-561
Total	1.49	1.43-1.55	-	-	1503	1435-1674	-	-	1.75	1.57-1.93	-	-	1818	1617-1908	-	-
Paramere	0.14	0.14-0.15	-	-	139	135-150	-	-	-	-	-	-	-	-	-	-
C.I.*	-				0.78 (0.76-0.81)				-				0.80 (0.79-0.82)			

*Cephalic Index (width : length).

F. arctica. Unlike *S. fraterculа*, this species did not exhibit such a well defined distribution on the hosts (Table 8). The majority of specimens (58.9%) on adult *F. arctica* were recovered from the back and breast (46.8% and 12.1% respectively), and while only 6.4% were found on the head, 34.3% were recovered from the neck. Therefore, a certain amount of overlap with *S. fraterculа* occurs in these regions. It is interesting to note that 80.4% of the specimens were recovered from the dorsal regions while *S. fraterculа* occupied mainly the ventral regions of the hosts. Nymphs represented only 11.4% of the *Q. helgovauki* population and again it appears that on adult hosts, adult Mallophaga either have low mortality or low reproductive rates. The sex ratio was nearly 1 : 1 (69 m : 71 f).

In contrast to the distribution on adult hosts, the majority of *Q. helgovauki* (93.2%) were recovered from the back and breast regions (65.2% and 28.0% respectively) of chicks (Table 9). Only 0.1% were found on the head regions, with 3.6% found on the neck regions. As on adult hosts, the majority (68.8%) were recovered from dorsal regions of the hosts. Nymphs represented 64.9% of the *Q. helgovauki* population, indicating that, as mentioned earlier, reproductive activity must occur on chicks. The sex ratio was 1 : 1.28 (56 m : 72 f).

From Fig. 5 it is evident that this species occurs in small numbers on adult hosts. At certain population

TABLE 8

DISTRIBUTION OF *QUADRACEPS HELGOVAUKI* ON ADULT *FRATERCULA ARCTICA**

Stage		Crown	Gular	Jugulum	Nape	Side of neck	Back	Breast
Nymph	No. hosts infested	1	1	1	3	0	3	1
	% Total infested.	16.7	16.7	16.7	50	0	50	16.7
	Total No. in region	2	2	1	7	0	4	2
	Mean.	2	2	1	2.3	0	1.3	2
	Range.	2	2	1	1-5	0	1-2	2
	% Total *Mallophaga* in region.	28.6	66.7	12.5	15.2	0	5.4	10.5
Male	No. hosts infested	2	0	3	2	0	8	2
	% Total infested.	18.2	0	27.3	18.2	0	72.7	18.2
	Total No. in region	3	0	4	16	0	40	6
	Mean.	1.5	0	1.3	8	0	5	3
	Range.	1-2	0	1-2	2-14	0	1-17	1-5
	% Total *Mallophaga* in region.	42.9	0	50	34.8	0	54.1	31.6
Female	No. hosts infested	2	1	1	3	1	9	3
	% Total infested.	16.7	8.3	8.3	25	8.3	75	25
	Total No. in region	2	1	3	23	1	30	11
	Mean.	1	1	3	7.7	1	3.3	3.7
	Range.	1	1	3	1-17	1	1-13	1-8
	% Total *Mallophaga* in region.	28.5	33.3	37.5	50	100	40.5	57.9
Total	No. hosts infested	2	1	3	4	1	10	3
	Total No. in region	7	3	8	46	1	74	19
	Mean.	3.5	3	2.7	11.5	1	7.4	6.3
	Range.	3-4	3	1-5	1-36	1	1-32	1-15
	% Total recovered.	4.5	1.9	5.1	29.1	0.1	46.8	12.1

*No specimens recovered from the auricular, side of neck, abdomen, legs and tail.

TABLE 9

DISTRIBUTION OF *QUADRACEPS HELGOVAUKI* ON *FRATERCULA ARCTICA* CHICKS*

Stage		Crown	Auricular	Nape	Back	Breast	Wing
Nymph	No. hosts infested.	0	0	2	10	4	1
	% Total infested.	0	0	20	100	40	100
	Total No. in region.	0	0	8	165	54	10
	Mean.	0	0	4	16.5	13.5	10
	Range.	0	0	4	1-90	3-30	10
	% Total *Mallophaga* in region.	0	0	61.5	69.3	52.9	100
Male	No. hosts infested.	1	1	1	7	6	0
	% Total infested.	12.5	12.5	12.5	87.5	75	0
	Total No. in region.	1	1	2	28	24	0
	Mean.	1	1	2	4	4	0
	Range.	1	1	2	1-11	1-12	0
	% Total *Mallophaga* in region.	100	100	15.4	11.8	23.5	0
Female	No. hosts infested.	0	0	2	10	7	0
	% Total infested.	0	0	20	100	70	0
	Total No. in region.	0	0	3	45	24	0
	Mean.	0	0	1.5	4.5	3.4	0
	Range.	0	0	1-2	1-14	1-9	0
	% Total *Mallophaga* in region.	0	0	23.1	18.8	23.5	0
Total	No. hosts infested.	1	1	2	11	7	1
	Total No. in region.	1	1	13	238	102	10
	Mean.	1	1	6.5	21.6	14.6	10
	Range.	1	1	6-7	1-115	1-51	10
	% Total recovered.	0.03	0.03	3.6	65.2	28.0	2.7

*No specimens recovered from the gular, jugulum, side of neck, abdomen, legs and tail.

densities, certain stages of *Q. helgovauki* even fail to occur. In spite of this, however, relationships did exist among the various stages of the population. Highly significant correlations were found between males and females, adults and nymphs, females and nymphs and males and nymphs ($r = 0.93^{***}$, df = 14; $r = 0.89^{***}$, df = 13; $r = 0.90^{***}$, df = 13 and $r = 0.84^{***}$, df = 11, respectively). These high correlations could be a reflection of the small numbers recovered. Interestingly, no significant correlation ($r = 0.11$ (N.C.), df = 12) existed between the populations of *Q. helgovauki* and *S. fratercula*. This is expected since the extent of their overlap on the hosts is small and should not encourage competition. The infestation of both species (Fig. 6) in relation to the total population indicates that both behave normally with increasing population density, remaining in essentially the same proportion throughout the population. The fluctuation at high population densities is undoubtedly due to the small number of hosts with high numbers of Mallophaga. This is expected of a population when no competition exists.

Table 10 gives the monthly infestation of *F. arctica* adults and chicks with *Q. helgovauki*. Specimens were first recovered from adult hosts during the last week of June in 1973, the first week in July of 1972. Its absence before this time cannot be explained, at present, although one may speculate that up until this time they may be present on the

FIGURE 6

The proportion of each mallophagan species on adult *Fratercula arctica*.

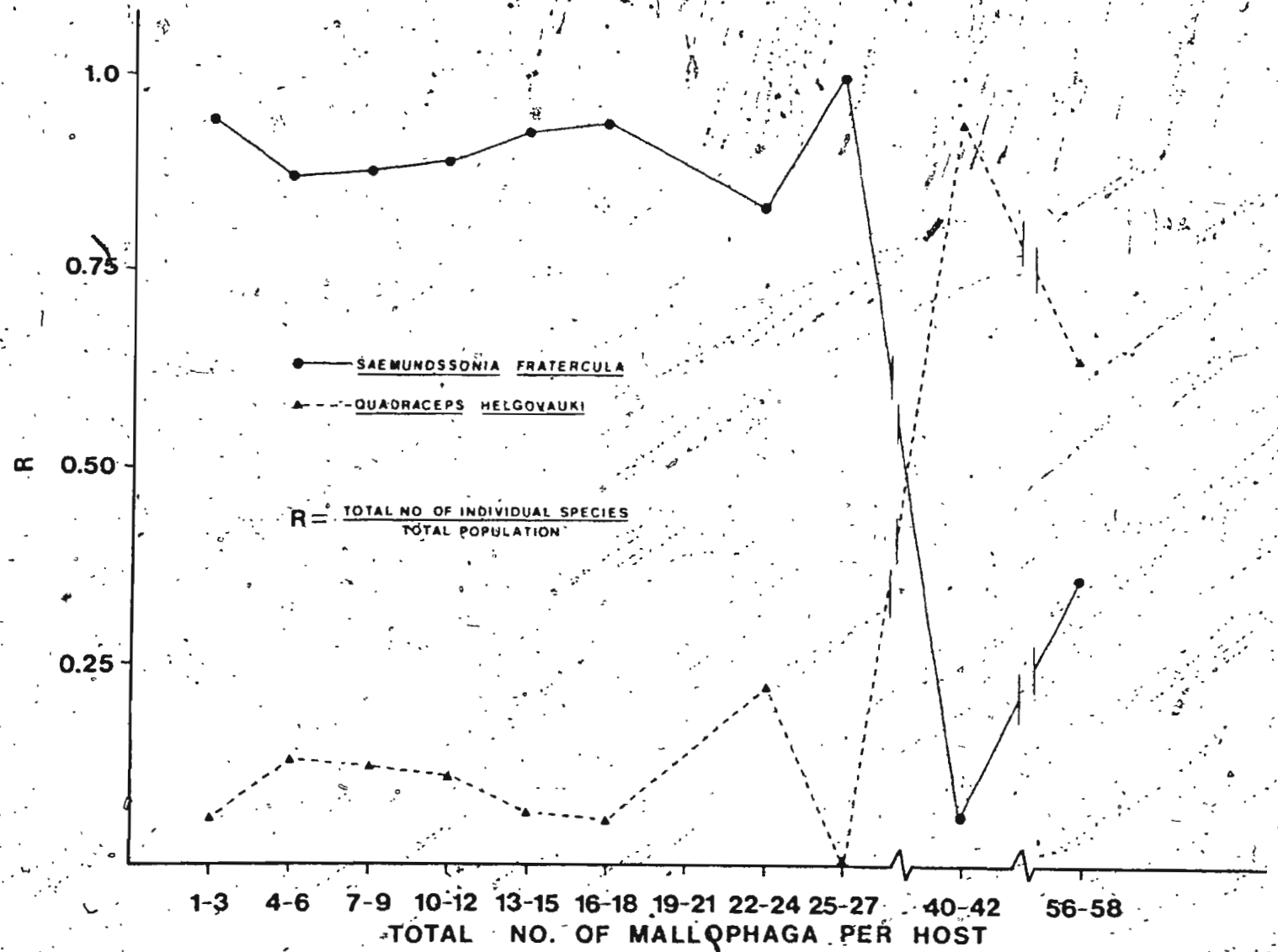

1.0
0.75
0.50
0.25
R
SAEMUNDSSONIA FRATERCULA
QUADRACEPS HELGOVAUKI
R = TOTAL NO OF INDIVIDUAL SPECIES / TOTAL POPULATION
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
40-42
56-58
TOTAL NO. OF MALLOPHAGA PER HOST

TABLE 10

MONTHLY INFESTATION OF *FRATERCULA ARCTICA* WITH *QUADRACEPS HELGOVAJKI*

	May		June		July		August		September	
	Adult	Chick	Adult	Chick	Adult	Chick	Adult	Chick	Adult	Chick
No. Host Examined	31	-	47	-	29	1	12	8	6	6
% Infested	0	-	16.6	-	24.1	100	16.7	75.0	33.3	66.7
Total No. recovered	0	-	42	-	70	37	4	159	42	169
Av. No. per infested host	0	-	8.4	-	10.0	37	2.0	26.8	21.0	42.3
Range	0	-	1-36	-	2-36	37	1-3	2-135	1-41	7-105
No. Males	0	-	16	-	37	10	0	18	16	28
No. Males per infested host	0	-	3.2	-	5.3	10	0	3.0	8.0	7.0
No. Females	0	-	22	-	27	10	2	22	20	40
No. Females per infested host	0	-	4.4	-	3.9	10	1.0	3.7	10.0	10
No. Nymphs	0	-	4	-	6	17	2	119	6	101
No. Nymphs per infested host	0	-	0.8	-	0.9	17	1.0	19.8	3.0	25.3

hosts in the egg stage, hatching in time for the transfer to chicks in July. Only one adult male specimen was recovered from one of the two adult hosts examined in December, the majority of specimens being *Austromenopon nigroplourum* and *S. fratercula*. It appears that this species may even overwinter in the egg stage as postulated by Boyd (1951) and Arora and Chopra (1957) for other mallophagan species. The infestation increased monthly until August, at which time it decreased sharply only to rise to a new peak in September. This closely follows the trend of the total population on the hosts during those months. The number of nymphs increased monthly, probably indicating that breeding must have occurred prior to this time.

The infestation of chicks with *Q. helgovauki* (Table 10) was highest in September and, in fact, the percentage of hosts infested was equal to that of *Saemundssonia fratercula* (Table 6). Interestingly the percentage of chicks infested decreased monthly while that of *S. fratercula* increased monthly (Table 6). This, coupled with the fact that few specimens of *Q. helgovauki* were recovered on adults during early winter, indicates that, as mentioned earlier, *S. fratercula* will be the dominant species in the spring and possibly only eggs of *Q. helgovauki* will be present on the hosts at that time.

Austromenopon nigropleurum (Denny, 1842)

This is a small amblyceran generally found running rapidly through the feathers or over the skin of the hosts. It is probably a blood feeder since most of the crops were either dark orange or red, the coloration probably being caused by ingested blood. Since very few specimens were encountered on *F. arctica*, observations on this species are scanty.

This species has previously been recorded from *Alca torda* (Emerson, 1972; Séguy, 1944; Timmermann, 1954a). However, Séguy (1944) and Zlotorzycka (1961) have recorded it from a wide variety of hosts. Eveleigh and Threlfall (1974) recently redescribed this species.

In the present study, specimens (1 per infested host) were recovered from 4 adult *F. arctica* (4.8%) which were also infested with other mallophagans. All specimens were female and were collected from the following regions: crown, gular, jugular and back. While this low infestation may be evidence of straggling amongst hosts of the colony, two adult *F. arctica* (in postnuptial plumage) examined in December were infested with mainly *A. nigropleurum* (67.1% of the total Mallophaga recovered). These *F. arctica* were probably from a different population, possibly from more northern regions, and such a high infestation with this species may possibly be typical of that population. However, the examination of more hosts during the winter months may

reveal that this species is common on adult *F. arctica* during those months. No specimens were recovered from *F. arctica* chicks. As reported by Ash (1960) and Touleshkov (1965), not all the species of Mallophaga recovered on particular hosts occur with equal frequency (Fig. 6). Of the 84 infested adult *F. arctica* only 15 (17.8%) were infested by more than one species of Mallophaga. Only 2 hosts (2.4%) were infested with all three species. The most frequent combinations were *S. fraterculа* and *Q. helgovauki* (11 hosts) while *S. fraterculа* and *A. nigropleurum* occupied only one host as did *Q. helgovauki* and *A. nigropleurum*.

Although, as mentioned previously, no correlation existed between the populations of *Q. helgovauki* and *S. fraterculа* on adult hosts, it was found that the various stages and sexes of the whole population of adult *F. arctica* were related. Males and females showed a high correlation ($r = 0.86^{***}$, df = 77) followed by adults and nymphs ($r = 0.36^{***}$, df = 73). Although not as highly correlated, females and nymphs and males and nymphs exhibited significant correlations ($r = 0.29^{*}$, df = 70 and $r = 0.34^{**}$, df = 74 respectively). Altogether it appears that while no relationship may exist between certain stages of the same species, and different species on a host, all stages of the total population show significant correlations. One explanation for this phenomenon could be similarities in the life-cycle (which are unknown) of the mallophagan species on adult *F. arctica*.

Several authors (Rothschild and Clay, 1961; Flint and Kostyrkc, 1967; Karpovich, 1970) have recorded *Ixodes uriae* from *F. arctica*. In the present study, specimens of *I. uriae* were recovered from twenty-three (18.4%) of the 125 adult *F. arctica* examined. The average number of specimens per infested bird was 15.6 (range 1 - 147).

Table 11 shows the monthly infestation of adult *F. arctica* with *I. uriae* during 1972 and 1973. The degree of infestation was higher in 1973 than 1972 (29.5% and 7.8% respectively). No ticks were recovered during May and September, very few in August with the majority being recovered early in July. In June the majority of specimens recovered were nymphs, while in July larvae were most common. Few adult females were recovered from adult *F. arctica* during the study.

No significant differences ($P > 0.05$) were found in the *I. uriae* burden of adult *F. arctica* with regard to sex and weight of the host.

The distribution of *I. uriae* on adult *F. arctica* is given in Table 12. Only 9.3% of the specimens were recovered from the head and neck regions with all the adult female specimens from these regions. The majority of ticks (88.2%) were recovered from the back, breast and abdomen, with 2.2% from the tail. Karpovich (1970) reported that

TABLE 11

MONTHLY INFESTATION OF ADULT *FRATERCULA ARCTICA* WITH *IXODES URIAE* DURING 1972 AND 1973

	May		June		July		August		September	
	1972	1973	1972	1973	1972	1973	1972	1973	1972	1973
No. Hosts	20	0	17	30	11	18	10	2	6	-
% Infested	0	0	11.7	36.7	18.2	38.8	10.0	0	0	-
No. Ticks	0	0	2	37	6	312	1	0	0	-
Av. No. per infested host	0	0	1	3.4	3.0	44.6	1	0	0	-
Range	0	0	1	1-7	1-5	1-147	1	0	0	-
No. Larvae	0	0	0	10	1	295	0	0	0	-
No. Nymphs	0	0	0	26	2	17	1	0	0	-
No. Females	0	0	2	1	3	0	0	0	0	-

TABLE 12

DISTRIBUTION OF *IXODES URIAE* ON ADULT *FRATERCULA ARCTICA**

Stage		Crown	Auricular	Nape	Side/neck	Back	Breast	Abdomen	Tail
Larva	No. hosts infested.	3	1	3	0	5	5	3	2
	% Total infested.	30	10	30	0	50	50	30	20
	Total No. in region	12	1	5	0	145	102	35	6
	Mean.	4	1	1.7	0	29	20.4	11.7	3.0
	Range.	1-6	1	1-3	0	1-95	1-56	1-32	1-5
	% Total *Mallophaga* in region.	46.1	100	71.4	0	92.9	89.5	79.5	75
Nymph	No. hosts infested.	6	0	1	0	7	5	3	1
	% Total infested.	37.5	0	6.3	0	43.7	31.3	18.8	6.3
	Total No. in region	11	0	1	0	11	12	9	2
	Mean.	1.8	0	1	0	1.6	2.4	3	2
	Range.	1-2	0	1	0	1-4	1-4	1-6	2
	% Total *Mallophaga* in region.	42.6	0	14.3	0	7.1	10.5	20.5	25
Female	No. hosts infested.	3	0	1	1	0	0	0	0
	% Total infested.	75	0	25	25	0	0	0	0
	Total No. in region	3	0	1	2	0	0	0	0
	Mean.	1	0	1	2	0	0	0	0
	Range.	1	0	1	2	0	0	0	0
	% Total *Mallophaga* in region.	11.5	0	14.3	100	0	0	0	0
Total	No. hosts infested.	9	1	4	1	8	7	6	2
	Total No. in region	26	1	7	2	156	114	44	8
	Mean.	2.9	1	1.8	2	19.5	16.3	7.3	4
	Range:	1-6	1	1-3	2	1-99	1-60	1-32	3-5
	% Total recovered.	7.2	0.03	2.0	0.06	43.8	32.0	12.4	2.2

*No specimens recovered from the gular, jugulum, wings and legs.

nymphs localized around the eyes of *Uria lomvia* but in this study only 23.9% of the nymphs occupied regions around the eye. No definite preference was shown for dorsal and ventral regions of the hosts as reported by Karpovich (1970) for nymphs on *U. lomvia*.

Nymphs and larvae were recovered mainly from the body regions of the hosts (69.6% and 92.1% respectively). Larvae were the dominant stage, representing 85.4% of the population followed by nymphs (12.8%). Only 1.7% of the population were females.

Flint and Kostyrkc (1967) and Karpovich (1970) reported the role of fledglings as hosts of different tick stages at different times of the year, noting that they play the major role in feeding during the second half of the summer in relation to different times of completing metamorphosis. No ticks were recovered from chicks at any month in the present study probably indicating that *F. arctica* chicks play a minor role in the tick life cycle in Newfoundland.

Waterston (1914) reported that the presence of large numbers of *I. uriae* on hosts adversely affects the mallophagan population on these hosts. In the present study, this effect was not observed.

Two specimens of *Alloptes fraterculae* (?) Dubinin, 1952 were recovered from *F. arctica*--one specimen from the back of a chick and the other from the gular region of an adult host. Belopolskaya (1952) reported that 64.0% of the *F. arctica* examined in the U.S.S.R. were infested with this species of feathermite. The precise taxonomic determination of this species is practically impossible, Atyeo (pers. comm.) reporting that this genus is badly in need of revision.

B. Common Murre (*Uriae aalge* (Pont.))

Belopolskaya (1947; *vide* Uspenskii, 1956) reported that *U. aalge* in Seven Islands, on the east Murman coast, U.S.S.R., were infested by six species of ectoparasites. The present author is unaware whether this included all groups of ectoparasites or just Mallophaga, although the former seems more probable.

In the present study, specimens of *Saemundssonia calva* (Kellogg, 1896), *Quadraceps obliquus* (Mjöberg, 1910) and *Austromenopon uriae* Timmermann, 1954 were recovered from *U. aalge*. Details of the infestation are given in Table 13 and the frequency distribution of each species in Fig. 7. It is evident that the distribution of Mallophaga on *U. aalge* is quite different from that of *F. arctica* (see Figs. 3 and 4), the former species exhibiting a greater

TABLE 13

DETAILS ON THE INFESTATION OF ADULTS AND CHICKS OF *URIA AALGE* WITH MALLOPHAGA

Age	No. examined	Percent infested	Mean	Range
Adult	28	82.1	10.2	1 - 53
Chick	6	83.3	35.8	20 - 59

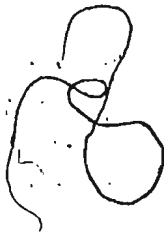
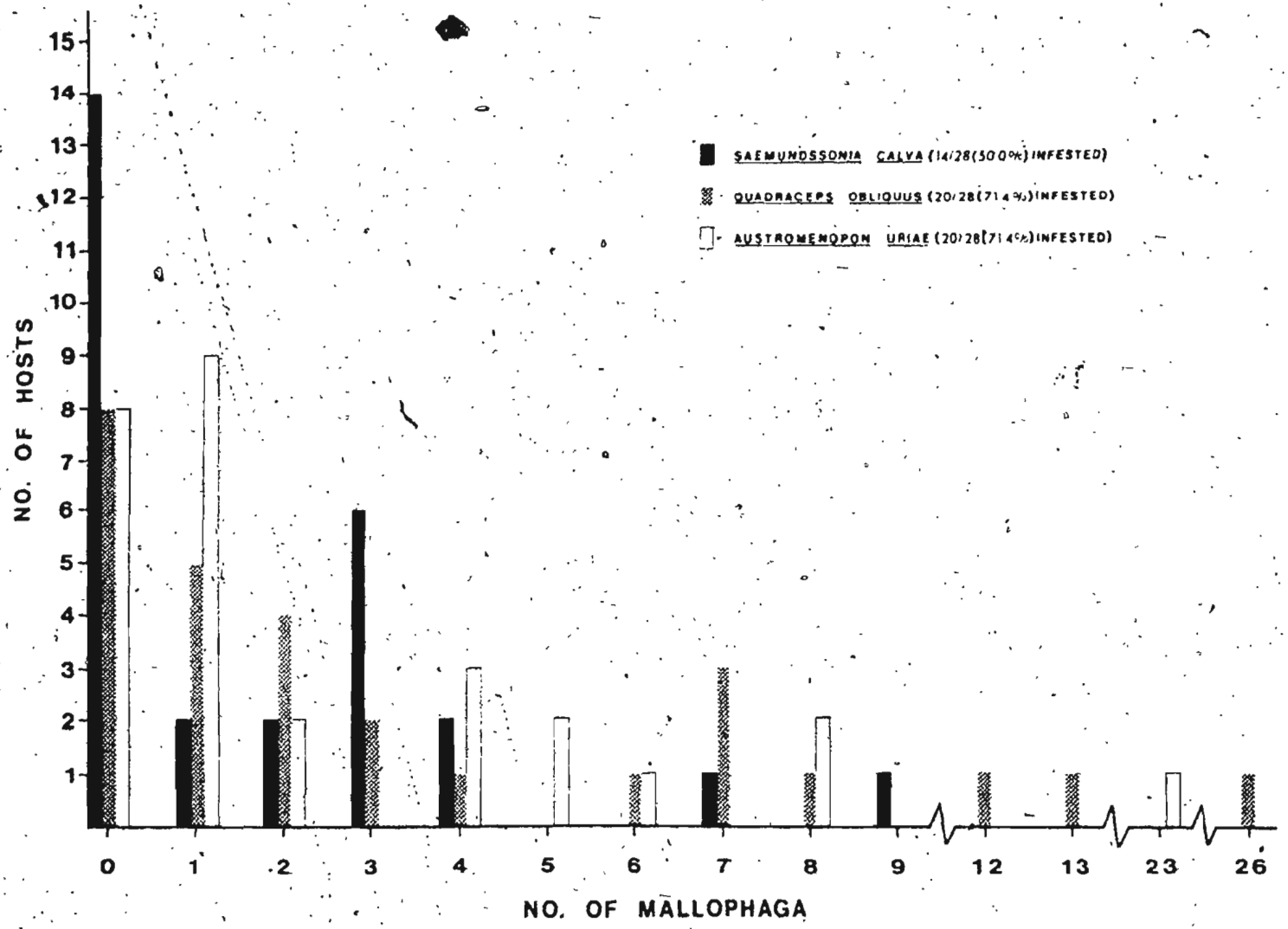


FIGURE 7

The frequency distribution of each mallophagan species on adult *Uria aalge*.


SAEMUNDSSONIA CALVA (14/28(50.0%) INFESTED)
QUADRACEPS OBLIQUUS (20/28(71.4%) INFESTED)
AUSTROMENOPON URIAE (20/28(71.4%) INFESTED)
NO. OF HOSTS
NO. OF MALLOPHAGA
0 1 2 3 4 5 6 7 8 9 12 13 23 26

degree and extent of infestation.

No significant difference ($P > 0.05$) was found in the mallophagan populations in 1972 and 1973, nor were significant differences ($P > 0.05$) found in the mallophagan burden of adult *U. aalge* with regard to sex and weight. The unavailability of *U. aalge* during certain months makes it impossible to give an account of the monthly infestation and the transfer of mallophaga from chicks-to-adults.

Saemundssonia calva (Kellogg, 1896)

This ischnoceran is basically similar to *Saemundssonia fratercula* with respect to habits and position on hosts.

S. calva has previously been reported from *U. aalge* in Europe (Timmermann, 1957) and North America (Emerson, 1972). In the present study, it was found on 56.5% of the infested adult birds with an average infestation of 1.9 (1 - 9) parasites per infested bird. *S. calva* were always found in mixed infestations with other mallophagan species. In contrast to *S. fratercula* on adult *F. arctica*, the frequency distribution (Fig. 7) was not of the "hollow curve" type, nor was it the dominant species on *U. aalge*.

All stages (except eggs) were found on the hosts. Like *Saemundssonia fratercula* (Table 4) this species can be accurately termed "head" louse, 93.4% being recovered from the head and neck regions of adult hosts (Table 14). On the head, 48.9% occupied the auricular region, 6.7% the

TABLE 14

DISTRIBUTION OF *SAEMUNDSSONIA CALVA* ON ADULT *URIA AALGE*

Stage		Crown	Auri-cular	Gular	Jugu-lar	Nape	Side/ neck	Back	Breast
Nymph	No. hosts infested.	0	6	1	2	0	1	2	0
	% Total infested.	0	60	10	20	0	10	20	0
	Total No. in region	0	13	1	2	0	1	2	0
	Mean.	0	2.2	1	1	0	1	1	0
	Range.	0	1-4	1	1	0	1	1	0
	% Total *Mallophaga* in region.	0	59.1	33.3	28.6	0	50	10	0
Male	No. hosts infested.	0	3	2	2	4	1	0	0
	% Total infested.	0	27.3	18.2	18.2	36.4	9.1	0	0
	Total No. in region	0	5	2	2	5	1	0	0
	Mean.	0	1.7	1	1	1.3	1	0	0
	Range.	0	1-3	1	1	1-2	1	0	0
	% Total *Mallophaga* in region.	0	22.7	66.7	28.6	71.4	50	0	0
Female	No. hosts infested.	1	3	0	1	2	0	0	1
	% Total infested.	12.5	37.5	0	12.5	25	0	0	12.5
	Total No. in region	1	4	0	3	2	0	0	1
	Mean.	1	1.3	0	3	1	0	0	1
	Range.	1	1-2	0	3	1	0	0	1
	% Total *Mallophaga* in region.	100	18.2	0	42.8	28.6	0	0	100
Total	No. hosts infested.	1	7	2	3	5	1	2	1
	Total No. in region	1	22	3	7	7	2	2	1
	Mean.	1	3.1	1.5	2.3	1.4	2	1	1
	Range.	1	1-7	1-2	1-5	1-3	2	1	1
	% Total recovered.	2.2	48.9	6.7	15.6	15.6	4.4	4.4	2.2

*No specimens were recovered from the abdomen, wings, legs and tail.

gular and only 2.2% the crown. On the neck, 15.6% were recovered from the jugulum and 15.6% and 4.4% from the nape and sides of the neck respectively. Unlike *S. fratercula*, only 22.3% of the specimens were recovered from the ventral regions of the head and neck. Only 4.4% and 2.2% were recovered from the back and breast respectively. Nymphs represented 42.2% of the *S. calva* population, being slightly higher than that reported for *S. fratercula* on adult hosts.

The population structure of *S. calva* in relation to the total population on adult hosts is illustrated in Fig. 8. Unlike *S. fratercula* on *F. arctica* (Fig. 5), no significant correlations existed between any of the stages on the hosts ($r = 0.15$ (N.C.), df = 11 for males and females; $r = 0.14$ (N.C.), df = 11 for males and nymphs; $r = 0.35$ (N.C.), df = 11 for adults and nymphs. The reason for this remains unclear but may be attributed to low numbers recovered. The sex ratio on adult *U. aalge* was 1 : 0.73 (15 m : 11 f.), Waterston (1914) reported that the sex ratio of *S. calva* on hosts in Britain was 2 : 3. This difference may be due to genetic isolation.

The ratio of *S. calva* in relation to the total population (Fig. 9) indicates that this species behaves "normally" with increasing population density, remaining in somewhat constant proportions throughout. No *S. calva* was recovered from *U. aalge* chicks.

FIGURE 8

The population structure of each mallophagan species in relation to the total population on adult *Uria aalge*.

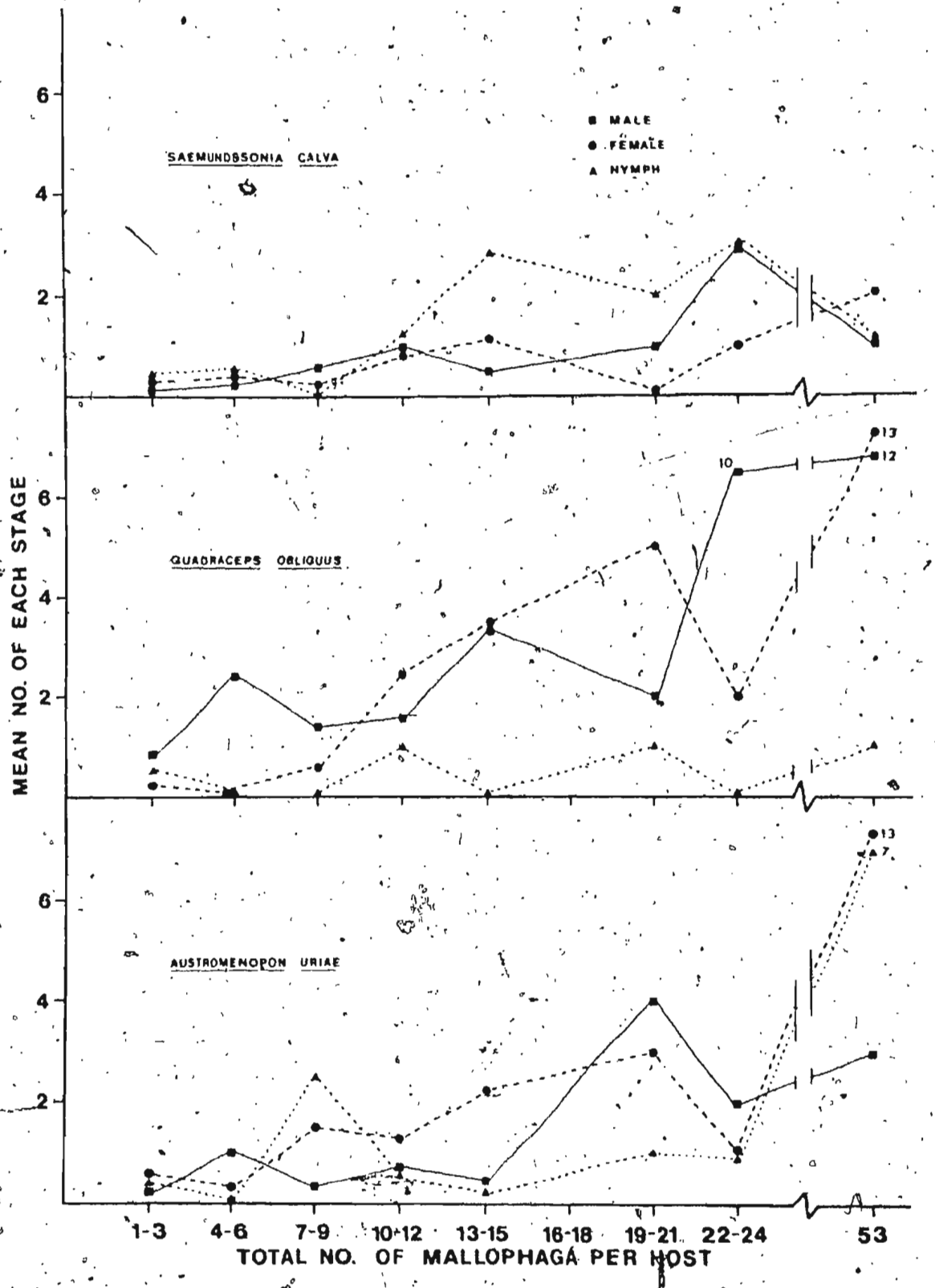
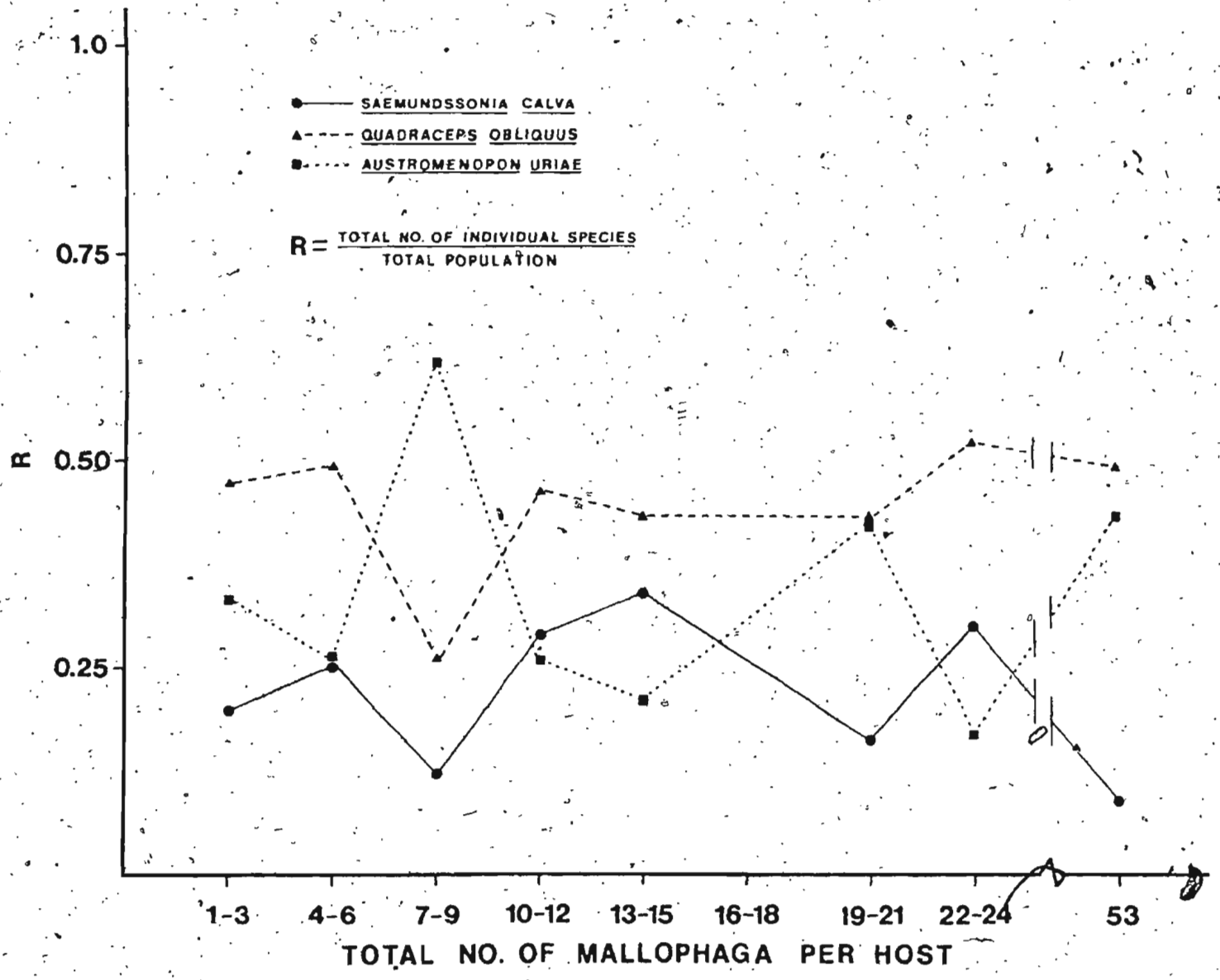

MALE
FEMALE
NYMPH
SAEMUNDSSONIA CALVA
QUADRACEPS OBLIQUUS
AUSTROMENOPON URIAE
MEAN NO. OF EACH STAGE
TOTAL NO. OF MALLOPHAGA PER HOST
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
53

FIGURE 9.

The proportion of each mallophagan species on adult *Uria aalge*.


1.0
0.75
0.50
0.25
R
SAEMUNDSSONIA CALVA
QUADRACEPS OBLIQUUS
AUSTROMENOPON URIAE
R = TOTAL NO. OF INDIVIDUAL SPECIES / TOTAL POPULATION
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
53
TOTAL NO. OF MALLOPHAGA PER HOST

Quadraceps obliquus (Mjöberg, 1910)

This ischnoceran has previously been recovered from *U. aalge* in Europe (Timmermann, in litt.), Russia (Belopolskaya, 1952) and North America (Emerson, 1972). In the present study, 86.9% of the infested adult *U. aalge* harboured this species, three hosts (13.1%) having this species as their sole mallophagans. The average number of lice per infested host was 4.7 (1 - 26). From the frequency distribution (Fig. 8) it is evident that the distribution is of the "hollow curve" type and that *Q. obliquus* is a dominant species on *U. aalge*, unlike *Q. helgovauki* on *F. arctica* (Fig. 6). One *U. aalge* examined in December harboured mainly *Quadraceps obliquus* (71.4% of the total population).

All infested *U. aalge* chicks harboured *Q. obliquus* with an average number of 20 (4 - 39) lice per infested chick. *Q. obliquus* were always found in mixed infestations with other mallophagan species.

All stages (except eggs) were recovered from *U. aalge*. Table 15 details the distribution of the stages and sexes of *Quadraceps obliquus* on adult *U. aalge*. Unlike *S. calva* (Table 14), the majority of specimens were recovered from body regions; 43.1% and 44.0% from the back and breast respectively. Only 2.7% were recovered from the head and 1.8% from the neck. 7.4% of the specimens (all adults) were found on the wings and 0.9% on the tail. Thus, there

TABLE 15

DISTRIBUTION OF *QUADRACEPS OBLIQUUS* ON ADULT *URIA AALGE**

Stage		Crown	Jugu-lum	Nape	Rack	Breast	Wings	Tail
Nymph	No. hosts infested.	1	0	1	4	1	0	0
	% Total infested.	16.7	0	16.7	66.7	16.7	0	0
	Total No. in region	1	0	1	4	2	0	0
	Mean.	1	0	1	1	2	0	0
	Range.	1	0	1	1	2	0	0
	% Total *Mallophaga* in region.	50	0	50	8.5	4.2	0	0
Male	No. hosts infested.	0	0	0	10	9	2	1
	% Total infested.	0	0	0	66.7	60	13.4	6.7
	Total No. in region	0	0	0	24	25	5	1
	Mean.	0	0	0	2.4	2.8	2.5	1
	Range.	0	0	0	1-7	1-10	2-3	1
	% Total *Mallophaga* in region.	0	0	0	51.1	52.1	62.5	100
Female	No. hosts infested.	1	1	1	8	7	2	0
	% Total infested.	10	10	10	80	70	20	0
	Total No. in region	1	1	1	19	21	3	0
	Mean.	1	1	1	2.4	3	1.5	0
	Range.	1	1	1	1-6	1-7	1-2	0
	% Total *Mallophaga* in region.	50	100	50	40.4	43.7	37.5	0
Total	No. hosts infested.	1	1	1	15	11	2	1
	Total No. in region	2	1	2	47	48	8	1
	Mean.	2	1	2	3.1	4.4	4	1
	Range.	2	1	2	1-14	1-12	3-5	1
	% Total recovered.	1.8	0.9	1.8	43.1	44	7.4	0.9

*No specimens were recovered from the auricular, gular, side of neck, abdomen, legs.

was little overlap with *S. calva* on the hosts. No definite preference was shown for dorsal and ventral regions of the hosts although slightly more specimens were recovered from dorsal regions. Unlike *S. calva*, only 7.3% of the specimens recovered were nymphs. It appears that *Quadraceps* spp. have low reproductive activity on adult hosts since *Quadraceps helgovauki* on adult *F. arctica* showed similar results. The sex ratio of *Q. obliquus* was 1 : 0.84 (55 m : 46 f).

Only 73.0% of *Q. obliquus* were from body regions of *U. aalge* chicks; 36% recovered from the back and 37% from the breast (Table 16). Only 1% was recovered from the head, while 14% were recovered from the neck. 4% (all adults) were recovered from the wings and 8% from the tail. Although only 31% of the specimens were nymphs, it appears that more breeding of this species occurs on chicks than on adults. The sex ratio was 1 : 1.47 (28 m : 41 f). This corresponds well with the data for *Q. helgovauki* on *F. arctica* chicks (Table 9).

The population structure of *Q. obliquus* (Fig. 8) shows that males and females follow similar patterns throughout the population and were found to exhibit a highly significant degree of relationship ($r = 0.59^{***}$, df = 17). No significant correlations, however, were found between males and nymphs (r = 0.07 (N.C.), df = 17, females and nymphs (r = 0.34 (N.C.), df = 17) and adults and nymphs (r = 0.13 (N.C.), df = 17). These latter correlations could be the

TABLE 16

DISTRIBUTION OF *QUADRACEPS OBLIQUUS* ON *URIA AALGE* CHICKS*

Stage		Auricular	Nape	Back	Breast	Wings	Tail
Nymph	No. hosts infested.	1	3	3	4	0	1
	% Total infested.	20	60	60	80	0	20
	Total No. in region.	1	4	14	11	0	1
	Mean.	1	1.3	4.7	2.8	0	1
	Range.	1	1-2	1-8	2-3	0	1
	% Total *Mallophaga* in region.	100	28.6	38.9	29.7	0	12.5
Male	No. hosts infested.	0	4	2	4	2	0
	% Total infested.	0	80	40	80	40	0
	Total No. in region.	0	7	9	10	2	0
	Mean.	0	1.8	4.5	2.5	1	0
	Range.	0	1-3	4-5	1-5	1	0
	% Total *Mallophaga* in region.	0	50	25	27	50	0
Female	No. hosts infested.	0	2	4	4	1	2
	% Total infested.	0	40	80.0	80	20	40
	Total No. in region.	0	3	13	16	2	7
	Mean.	0	1.5	3.3	4	1	3.5
	Range.	0	1-2	1-7	1-9	1	3-4
	% Total *Mallophaga* in region.	0	21.4	36.1	43.3	50	87.5
Total	No. hosts infested.	1	5	4	4	2	2
	Total No. in region.	1	14	36	37	4	8
	Mean.	1	2.8	9	9.3	2	4
	Range.	1	1-5	1-17	5-12	1-3	4
	% Total recovered.	1	14	36	37	4	8

*No specimens recovered from the crown, gular, jugulum, side of neck, abdomen, and legs.

result of few nymphs in the population.

The ratio of *Q. obliquus* in relation to the total population (Fig. 9) shows that the proportion of this species, like *S. calva*, is relatively constant at various levels of population density. This is what one would expect from a "normal" population where competition with other species does not occur.

Austromenopon uriae Timmermann, 1954

This extremely active amblyceran was found mainly on the skin of the hosts although occasionally they could be seen running through and over the feathers; Ash (1960) noted that amblycerans were the first to transfer to new hosts. *A. uriae* will transfer to one's hand very quickly on handling a bird. Lice were frequently seen resting on the eyelids with their heads between the eye and the eyelid. No other species on *U. aalge* were observed in this position. Whether this species supplements its diet with liquid eye secretions is not known, but such a diet has been postulated for the nymphal stages of *Dennyus truncatus* on the swift (Rothschild and Clay, 1961). The crops of many specimens were red in color, probably indicating that this is, in some way, dependent on blood.

A. uriae has previously been recorded from *U. aalge* in Europe (Timmerman, 1954) and North America (Emerson, 1972). In the present study, 86.9% of the infested adult

hosts harboured this species. Only 1 host (4.3%) had this species as its sole mallophagan. The average number per infested host was 3.5 (1 - 23) lice. Like *Quadraceps obliquus*, the frequency-distribution (Fig. 7) indicates that it is also a dominant species on *U. aalge*, occurring with the same frequency as the former species. One adult *U. aalge* captured in December harboured no *A. uriae*.

Similar to *Quadraceps obliquus*, all *U. aalge* chicks infested with Mallophaga harboured *A. uriae*. The average number per infested chick was 15.8 (11 - 21) lice.

The distribution of *A. uriae* on adult hosts is given in Table 17. Unlike *S. calva* and *Q. obliquus*, *A. uriae* does not exhibit such a well defined distribution on adult hosts. Although the majority of specimens (71.3%) were found on body regions (18.8% on the back and 52.5% on the breast), all head and neck regions harboured this species, 8.8% being recovered from the head and 19.1% from the neck. As noted by Ash (1960), amblycerans may be found on any region of the host's body. *A. uriae* certainly exhibits this characteristic, although the breast region is preferred. Only 27.5% of the population were nymphs probably indicating that like the *Saemundssonia* and *Quadraceps* spp., *Austromenopon* spp. also have low adult mortality rates or low reproductive activity on adult hosts. The sex ratio was 1 : 2.11 (18 m : 38 f) indicating that females live twice as long as males, assuming that one insemination is sufficient.

TABLE 17

DISTRIBUTION OF *AUSTROMENOPON URIAE* ON ADULT *URIA AALGE**

Stage		Crown	Auricular	Gular	Jugulum	Nape	Side/neck	Back	Breast
Nymph	No. hosts infested.	0	0	2	0	1	1	4	6
	% Total infested.	0	0	18.2	0	9.1	9.1	36.4	54.5
	Total No. in region	0	0	2	0	1	1	4	14
	Mean.	0	0	1	0	1	1	1	2.3
	Range.	0	0	1	0	1	1	1	1-7
	% Total *Mallophaga* in region.	0	0	66.7	0	9.1	33.3	26.7	33.3
Male	No. hosts infested.	1	1	1	0	3	0	1	7
	% Total infested.	11.1	11.1	11.1	0	33.3	0	11.1	77.7
	Total No. in region	1	1	1	0	5	0	1	10
	Mean.	1	1	1	0	1.7	0	1	1.4
	Range.	1	1	1	0	1-2	0	1	1-2
	% Total *Mallophaga* in region.	50	50	33.3	0	45.4	0	6.7	23.8
Female	No. hosts infested.	1	1	0	2	4	2	6	8
	% Total infested.	6.3	6.3	0	12.5	25	12.5	37.5	50
	Total No. in region.	1	1	0	2	5	2	10	18
	Mean.	1	1	0	1	1.3	1	1.7	2.3
	Range.	1	1	0	1	1-2	1	1-4	1-8
	% Total *Mallophaga* in region.	50	50	0	100	45.5	66.7	66.7	42.9
Total	No. hosts infested.	2	2	3	2	4	2	8	12
	Total No. in region	2	2	3	2	11	3	15	42
	Mean.	1	1	1	1	2.5	1.5	1.9	3.5
	Range.	1	1	1	1	1-5	1-2	1-5	1-17
	% Total recovered.	2.5	2.5	3.8	2.5	13.8	3.8	18.8	52.5

*No specimens recovered from the abdomen, wings, tail and legs.

A. uriae on chicks was recovered mainly from the head and neck, 51.9% being recovered from the head and 27.8% from the neck (Table 18). The majority of specimens (31.6%) on the head were from the crown, while on the neck, the majority (25.3%) were from the nape. Of the 20.3% recovered from the body regions, 16.5% were from the breast, 1.3% from the abdomen and 2.5% from the back. The dorsal regions of the hosts were preferred, 59.4% of the body dwellers being recovered from there. Nymphs were the dominant stage on chicks, representing 51.8% of the *A. uriae* population. This probably indicates that this species have greater reproductive activity on these hosts. The sex ratio was 1 : 1.38 (16 m : 22 f).

From Fig. 8 it is evident that the *A. uriae* population on adult *U. aalge* is similar to that of *Q. obliquus*. Males and females follow similar patterns throughout the population and were found to exhibit a significant correlation ($r = 0.55^{*}$, df = 18). Significant correlations also existed between adults and nymphs and females and nymphs ($r = 0.73^{***}$, df = 18 and $r = 0.79^{***}$, df = 18, respectively). No correlation, however, was found between males and nymphs ($r = 0.35$ (N.C.), df = 18) of the population. Similar to *S. calva* and *Q. obliquus*, the ratio of *A. uriae* at different levels of population density (Fig. 9) was relatively constant as one would expect in a "normal" population.

From Figs. 7 and 8 it is apparent that not all species

TABLE 18

DISTRIBUTION OF *AUSTROMENOPON URIAE* ON *URIA AALGE* CHICKS*

Stage		Crown	Auricular	Gular	Jugulum	Nape	Back	Breast	Abdomen
Nymph	No. hosts infested.	4	3	1	1	5	1	3	1
	% Total infested.	80	60	20	20	100	20	60	20
	Total No. in region	9	7	3	2	13	1	5	1
	Mean.	2.3	2.3	3	2	2.6	1	1.7	1
	Range.	1-4	2-4	3	2	1-4	1	1-3	1
	% Total *Mallophaga* in region.	36	58.3	75	100	65	50	38.5	100
Male	No. hosts infested.	4	1	0	0	2	1	3	0
	% Total infested.	80	20	0	0	40	20	60	0
	Total No. in region	7	2	0	0	3	1	3	0
	Mean.	1.8	2	0	0	1.5	1	1	0
	Range.	1-3	2	0	0	1-2	1	1	0
	% Total *Mallophaga* in region.	28	16.7	0	0	15	50	23.0	0
Female	No. hosts infested.	4	1	1	0	2	0	2	0
	% Total infested.	80	20	20	0	4	0	40	0
	Total No. in region	9	3	1	0	4	0	5	0
	Mean.	2.3	3	1	0	2	0	2.5	0
	Range.	1-3	3	1	0	1-3	0	2-3	0
	% Total *Mallophaga* in region.	36	25	25	0	20	0	38.5	0
Total	No. hosts infested.	4	2	2	1	5	1	3	1
	Total No. in region	25	12	4	2	20	2	13	1
	Mean.	6.3	6	2	2	4	2	4.3	1
	Range.	3-9	2-9	1-3	2	1-9	2	2-7	1
	% Total recovered.	31.6	15.2	5.1	2.5	25.3	2.5	16.5	1.3

*No specimens recovered from the side of neck, wings, tail and legs.

occur with equal frequency, of the 23 infested adult *U. aalge*, 19 (82.6%) were infested by more than one species of Mallophaga. This is a high number when compared with the infestation of adult *F. arctica*. Eight (34.7%) harboured two genera of Mallophaga while eleven (47.8%) harboured all three genera. Interestingly, no *U. aalge* were found to harbour only *Q. obliquus* and *S. calva*, these genera being frequently associated on *F. arctica*. Six hosts (26.1%) harboured *Q. obliquus* and *A. uriae* only, while only 2 hosts (8.7%) harboured only *S. calva* and *A. uriae*. Since overlap between the various species occurred in several regions, it would be expected that the population of one species could be affected by another. It was found that no significant correlations existed between *S. calva* ("head" lice) and either of *A. uriae* and *Q. obliquus* ("body" lice) ($r = 0.284$ (N.C.), $df = 21$ and $r = 0.277$ (N.C.), $df = 21$ respectively). A highly significant correlation, however, existed between *Q. obliquus* and *A. uriae* ($r = 0.705^{***}$, $df = 21$), both being body dwellers. This correlation is also obvious from Fig. 8, both species showing similar trends. This probably indicates that both species are affected by the same environmental conditions offered by the habitat. Since the correlation was positive, competition is not a significant factor. This is expected since one species is an amblyceran and the other an ischnoceran with different food preferences and undoubtedly different oviposition sites,

and behavior; hence, competition is not encouraged.

In spite of the fact that not all stages of a population and not all species are related on hosts, it was found that, as on *F. arctica*, the different stages of the whole population on *U. aalge* were related. Highly significant correlations were found between males and females ($r = 0.68^{***}$, $df = 21$), adults and nymphs ($r = 0.74^{***}$, $df = 21$) and females and nymphs ($r = 0.77^{***}$, $df = 21$). A significant correlation was also found between males and nymphs ($r = 0.55^{**}$, $df = 21$). As mentioned earlier for *F. arctica* one explanation for this phenomenon could be similarities in the life cycle of the mallophagan species (which are unknown) on adult *U. aalge*.

Rothschild and Clay (1961) noted that the population of lice may be large without apparently harming the bird, but when it is abnormally heavy, in sick, captive, or young birds, the effect on the host may be serious. In the present study, five *U. aalge* chicks, taken from their nests soon after hatching and reared in the laboratory for several weeks, were examined for Mallophaga. Four of the chicks harboured less than average infestations (25 (12-34) Mallophaga as compared to 35.8 (20-59) for wild chicks). However, one chick harboured 722 *Austromenopon uriae* specimens. The plumage of this bird was in a very frayed, ungroomed condition and at a very retarded stage of development. Accumulations of skin débris, sometimes red in

appearance (probably blood caused by excessive scratching), could be seen on many areas of the body, particularly the head. Several days prior to its death, the bird became very weak, refusing to eat. It is obvious that such a large number of *A. uriae* had a very pronounced effect on the health of the bird and undoubtedly contributed to its death. As on wild chicks, no *Saemundssonia calva* were recovered from experimental chicks, the majority being *A. uriae*.

Belopolskaya (1952) reported that 28% of the adult *U. aalge* and 100% of the chicks were infested with *Ixodes uriae* while Flint and Kostyrkc (1967) noted that *U. aalge* was the main host for *I. uriae* in Murman, U.S.S.R. (75% infested, average 8.1 specimens per infested host). Karpovich (1970) also reported that *U. aalge* was the main host of *I. uriae* on islands in East Murman, U.S.S.R. Clifford *et al.*, (1970) recovered *I. uriae* from this host taken on islands off the Oregon coast, U.S.A.

In the present study, specimens of *I. uriae* were recovered from fifteen (65.2%) of the 28 adult *U. aalge* examined. The mean number of specimens per infested host was 4.5 (1 - 25). Although *I. uriae* appears to prefer *U. aalge*, the incidence of infestation being higher than that on *F. arctica*, the intensity was much lower. It appears that this could be due to more *U. aalge* being more readily accessible to *Ixodes uriae* on the cliffs.

No significant difference ($P > 0.05$) was found in the infestation during the two years of this study nor were any differences found in the *I. uriae* burden of *U. algae* with regard to sex or weight of the host.

The majority of specimens of *I. uriae* (43.3%) were recovered from the neck of adult *U. algae* although none were recovered from the jugulum region (Table 19). The head harboured 21.0% of the specimens while 34.4% were from the body. Flint and Kostyrko (1967) reported that nymphs and female ticks frequently localized on the birds' heads (34%), necks (26.8%) and wings (26.8%), and less frequently near the anus (8.3%) and legs (4.1%). In the present study, no specimens were recovered from the wings and legs although one specimen (1.5%) was recovered from the tail. Karpovich (1970) also failed to find ticks on the featherless leg areas.

Nymphs were recovered mainly from the head and neck (90%), while larvae (63.7%) were reocvered from body regions; adult females were recovered only from the neck as on adult *F. arctica*. Karpovich (1970) reported that nymphs were mainly recovered from the back and less frequently from the abdomen, femur, beck and head while larvae localized on the back, neck, breast, femur and abdomen with adult females on the neck. Flint and Kostyrko (1967) reported that adult and nymphal ticks represented 50% and 44% of the total population on adult birds, while larvae were rarely found

TABLE 19

DISTRIBUTION OF *IXODES URIAE* ON ADULT *URIA AALGE**

Stage		Crown	Auricular	Gular	Nape	Side/neck	Back	Breast	Abdomen	Tail
Larva	No. hosts infested	1	0	0	4	2	3	2	1	0
	% Total infested.	10	0	0	40	20	30	20	12.5	0
	Total No. in region	1	0	0	6	4	14	4	1	0
	Mean.	1	0	0	1.5	2	4.7	2	1	0
	Range.	1	0	0	1-2	1-3	1-5	1-3	1	0
	% Total *Mallophaga* in region.	20	0	0	54.5	22.2	93.3	100	25	0
Nymph	No. hosts infested	2	1	1	3	2	1	0	2	1
	% Total infested.	25	12.5	12.5	37.5	25	12.5	0	20	12.5
	Total No. in region	4	8	1	3	11	1	0	3	1
	Mean.	2	8	1	1	5.5	1	0	1.5	1
	Range.	2	8	1	1	1-11	1	0	1-2	1
	% Total *Mallophaga* in region.	80	100	100	27.3	61.1	6.7	0	75	100
Female	No. hosts infested	0	0	0	2	3	0	0	0	0
	% Total infested.	0	0	0	40	60	0	0	0	0
	Total No. in region	0	0	0	2	3	0	0	0	0
	Mean.	0	0	0	1	1	0	0	0	0
	Range.	0	0	0	1	1	0	0	0	0
	% Total *Mallophaga* in region.	0	0	0	18.2	16.7	0	0	0	0
Total	No. hosts infested	2	1	1	8	4	4	2	3	1
	Total No. in region	5	8	1	11	18	15	4	4	1
	Mean.	2.5	8	1	1.4	4.5	3.8	2	1.3	1
	Range.	2-3	8	1	1-2	1-14	1-5	1-3	1-2	1
	% Total recovered.	7.5	12	1.5	16.4	26.9	22.4	6.0	6.0	1.5

*No specimens recovered from the jugulum, wings and legs.

(6%). In the present study, only 7.4% of the population recovered were adults, 44.7% were nymphs and 47.9% were larvae. Similar to the distribution on adult *F. arctica* (Table 12); no preference for dorsal or ventral regions of the hosts was noted although 46.3% of the population were recovered from dorsal regions. No differences were observed in the mallophagan populations on hosts infested with *I. uriae*. No ticks were recovered from *U. aalge* chicks.

C. Thick-billed Murres (*Uria lomvia* (L.))

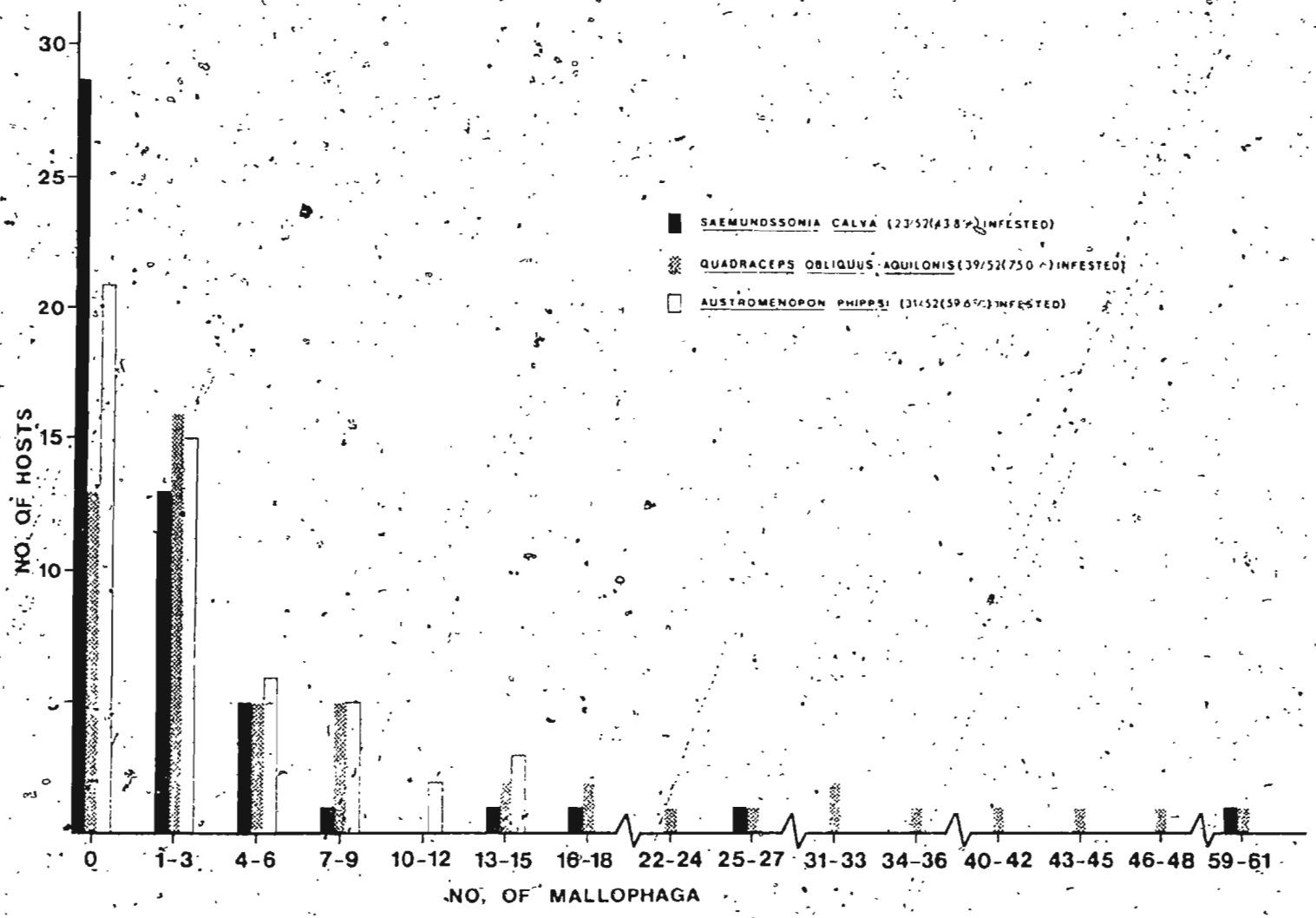
Markov (1937) noted changes in the population of mallophagans on *U. lomvia lomvia* related to the age of the host. Belopolskaya (1947; *vide* Uspenskii, 1956) reported that *U. lomvia* was infested with three species of ectoparasites. In the present study, specimens of *Saemundssonia calva* (Kellogg, 1896), *Quadraceps obliqua aquilonis* Timmermann (in litt.) and *Austromenopon phippsi* Eveleigh and Threlfall (1974) were recovered from *U. lomvia*.

Of the 52 specimens examined, forty-four (84.6%) were infested with Mallophaga; averaging 18.6 (1 - 76) lice per infested host. This is similar to the infestation of adult *U. aalge* (Table 13). The frequency distribution (Fig. 10) is also similar to that reported for *U. aalge* (Fig. 7).

No significant difference ($P > 0.05$) was found in the mallophagan burden of *U. lomvia* with regard to the sex of

FIGURE 10

The frequency distribution of each mallophagan species on adult *Uria lomvia*.


SAEMUNDSSONIA CALVA (23/52(43.8%) INFESTED)
QUADRACEPS OBLIQUUS AQUILONIS (39/52(75.0%) INFESTED)
AUSTROMENOPON PHIPPSI (31/52(59.6%) INFESTED)
NO. OF HOSTS
30
25
20
15
10
5
0
0
1-3
4-6
7-9
10-12
13-15
16-18
22-24
25-27
31-33
34-36
40-42
43-45
46-48
59-61
NO. OF MALLOPHAGA

the host. However, a highly significant correlation was found between the host weight and the infestation ($r = 0.543^{***}$, df = 49). The regression line of infestation on body weight (Fig. 11) shows that the infestation on *U. lomvia* decreases with increasing weight of the hosts. Since the hosts were collected in November and December, the sample was probably composed of fledglings as well as adult hosts, thus explaining the wide range of weights (Appendix 1). If weight can be assumed as an indicator of age, then the older the host, the smaller the mallophagan population.

The percentage of *U. lomvia* infested during November and December are identical (Table 20), but the average number of mallophagans per infested host greatly decreased in December. This decrease in infestation with time verifies the above hypothesis. One cannot discount the possibility, however, that this may a reflection of winter conditions on the mallophagan population although it is highly improbable. All the hosts were either in advanced stages of, or in full winter plumage.

Saemundssonia calva (Kellogg, 1896)

The recovery of *S. calva* from *U. lomvia* in North America constitutes a new geographical record as it has previously been recorded only from Europe (Timmermann, 1957).

FIGURE 11

Regression line of mallophagan infestation on body weight for *Uria lomvia*.

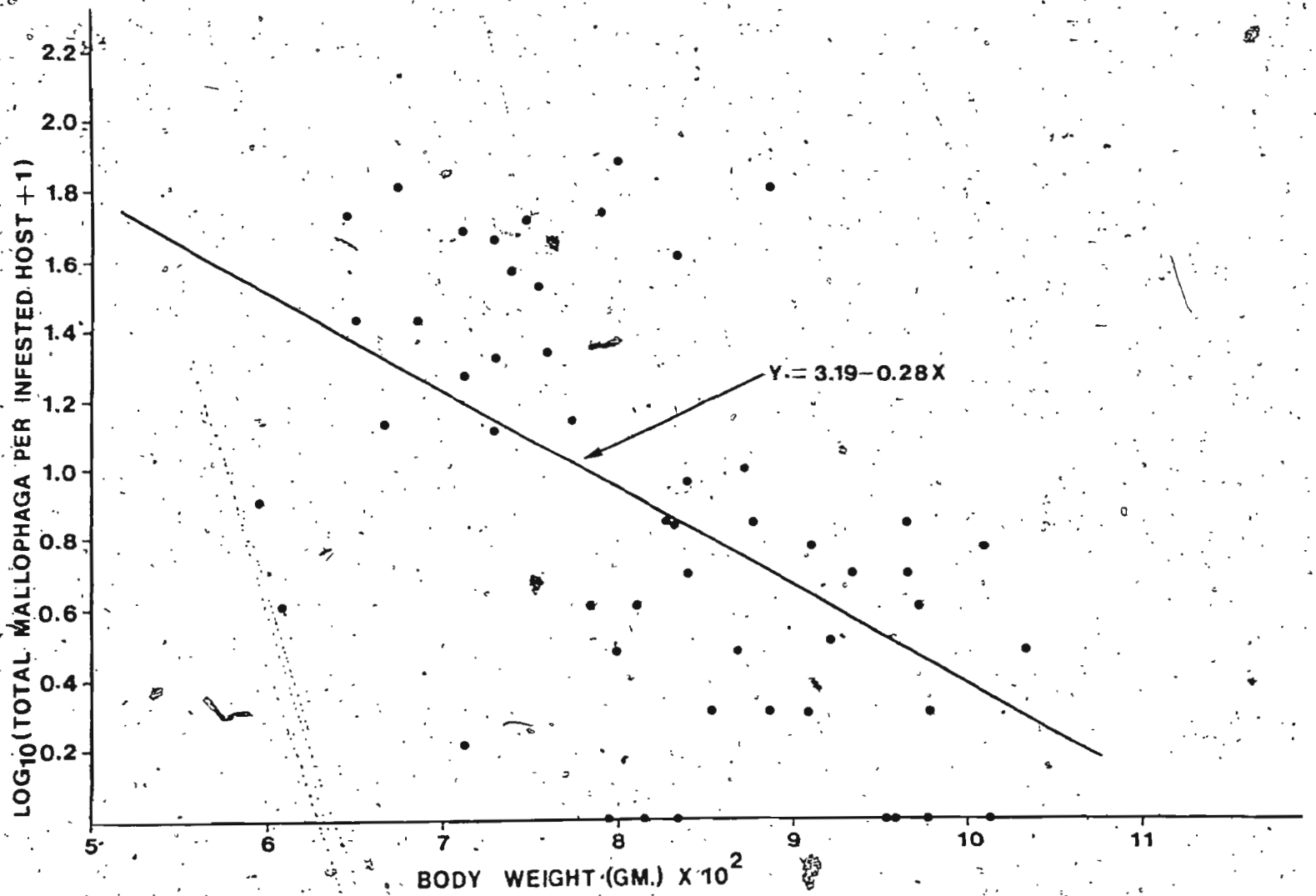

LOG10(TOTAL MALLOPHAGA PER INFESTED HOST +1)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
Y = 3.19 − 0.28X
5
6
7
8
9
10
11
BODY WEIGHT (GM.) X 10²

TABLE 20

DETAILS ON THE INFESTATION OF *URIA LOMVIA* DURING NOVEMBER AND DECEMBER, 1972

Month	No. Host examined	Percent infested	No. Mallophaga	Mean	Range
November	32	84.4	614	22.7	1 - 76
December	20	85.0	205	12.1	1 - 53

In the present study, 52.3% of the infested hosts harboured this species with an average of 3.9 (1 - 60) parasites per infested bird. Only one host was found to have *S. calva* as its sole mallophagan. As on *U. aalge* (Fig. 7), *S. calva* was not the dominant species on *U. lomvia* (Fig. 10). The percentage of infested hosts was similar on both hosts, although the intensity of infestation was higher on *U. lomvia*.

All stages (except eggs) were recovered from the hosts examined. The majority of specimens (88.3%) were found on the neck of the hosts, only 1.2% being recovered from the head (Table 21). No specimens were recovered from the auricular region, thus differing from the distribution of *S. calva* on *U. aalge* were 57.8% were recovered from the head with 48.9% from the auricular region. Only 10.4% were recovered from the body; 5.2% from both the back and breast. A slight preference (52.6%) was shown for the dorsal regions of the hosts. Nymphs represented 40.5% of the *S. calva* population (similar to that on *U. aalge*). The sex ratio was 1 : 1.19 (47 m : 56 f). On *U. aalge*, the males were dominant.

The population structure of *S. calva* in relation to the total population on *U. lomvia* is illustrated in Fig. 12. It is evident that the stages and sexes follow similar patterns throughout the population. Highly significant correlations were found between males and females

TABLE 21

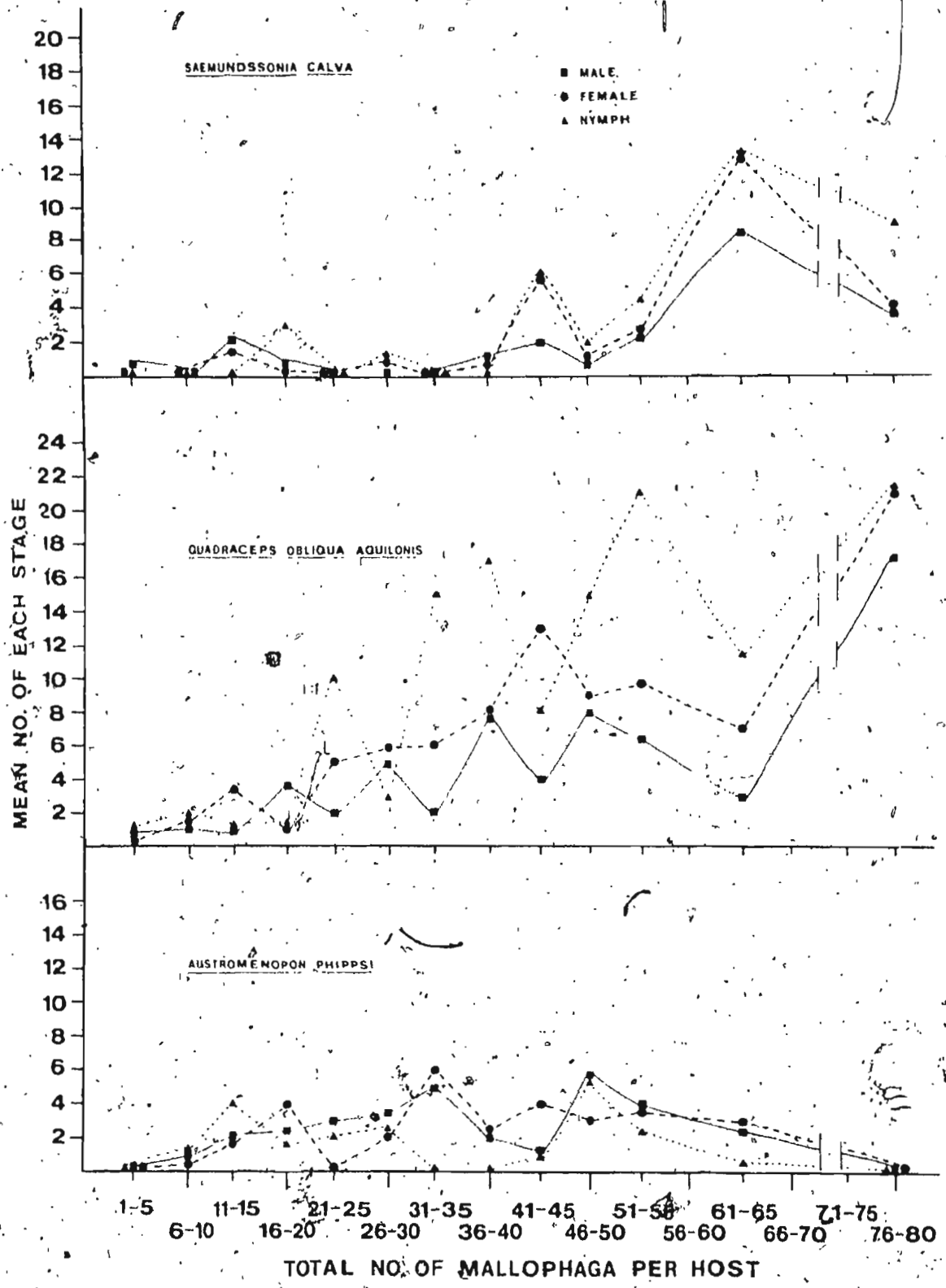
DISTRIBUTION OF *SAEMUNDSSONIA CALVA* ON *URIA LOMVIA* ADULTS*

Stage		Crown	Gular	Jugu-lum	Nape	Side/ neck	Back	Breast
Nymph	No. hosts infested.	0	1	5	8	0	2	1
	% Total infested.	0	8.3	41.6	66.7	0	16.7	8.3
	Total No. in region	0	1	32	32	0	4	1
	Mean.	0	1	6.4	4	0	2	1
	Range.	0	1	3-14	2-9	0	1-3	1
	% Total *Mallophaga* in region.	0	100	45.7	39.5	0	44.4	11.2
Male	No. hosts infested.	0	0	9	7	1	2	4
	% Total infested.	0	0	50	38.9	5.6	11.1	22.2
	Total No. in region	0	0	15	24	1	3	4
	Mean.	0	0	1.7	3.4	1	1.5	1
	Range.	0	0	1-4	1-11	1	1-2	1
	% Total *Mallophaga* in region.	0	0	21.4	29.6	50	33.4	44.4
Female	No. hosts infested.	1	0	7	7	1	1	3
	% Total infested.	7.7	0	53.8	53.8	7.7	7.7	23.1
	Total No. in region	1	0	23	25	1	2	4
	Mean.	1	0	3.3	3.6	1	2	1.3
	Range.	1	0	1-12	1-12	1	2	1-2
	% Total *Mallophaga* in region.	100	0	32.9	30.9	50	22.2	44.4
Total	No. hosts infested.	1	1	10	9	1	4	7
	Total No. in region	1	1	70	81	2	9	9
	Mean.	1	1	7.0	9	2	2.3	1.3
	Range.	1	1	1-30	3-30	2	1-3	1-2
	% Total recovered.	0.6	0.6	40.4	46.8	1.1	5.2	5.2

*No specimens recovered from the auricular, abdomen, wings, tail and legs.

FIGURE 12

The population structure of each mallophagan species in relation to the total population on adult *Uria lomvia*.


SAEMUNDSSONIA CALVA
MALE
FEMALE
NYMPH
QUADRACEPS OBLIQUA AQUILONIS
AUSTROMENOPON PHIPPSI
MEAN NO. OF EACH STAGE
1-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65
66-70
71-75
76-80
TOTAL NO. OF MALLOPHAGA PER HOST

($r = 0.96^{***}$, df = 21), adults and nymphs ($r = 0.90^{***}$, df = 21) and females and nymphs ($r = 0.90^{***}$, df = 21), while a slightly lower correlation was found between males and nymphs ($r = 0.88^{***}$, df = 21). In contrast, no correlations existed between the stages and sexes of *S. calva* on *U. aalge* (Fig. 8). The ratio of *S. calva* at different population densities (Fig. 13), indicates that there is a slight increase in the proportion of this species at high population densities. This could be a reflection of the fact that few hosts harbour large populations of Mallophaga.

The percentage of hosts infested with *S. calva* in November was lower than in December (Table 22), but the intensity of infestation was higher in November. In both months the proportion of the stages and sexes were similar, thus the reduction in the population is reflected equally throughout all stages.

Quadraceps obliqua aquilonis Timmermann (in litt.)

Markov (1937) and Belopolskaya (1952) reported *Quadraceps obliquus* from *U. lomvia* in Russia, Timmermann (1954, 1957) also reporting *Q. obliquus* from this host in Europe. Timmermann (in litt.) erected *Quadraceps obliqua aquilonis* as a new sub species of *Quadraceps obliquus* on the basis of its larger size. In the present study, *Q. obliqua aquilonis* was recovered from *U. lomvia*, constituting

FIGURE 13

The proportion of each mallophagan species on adult *Uria lomvia*.

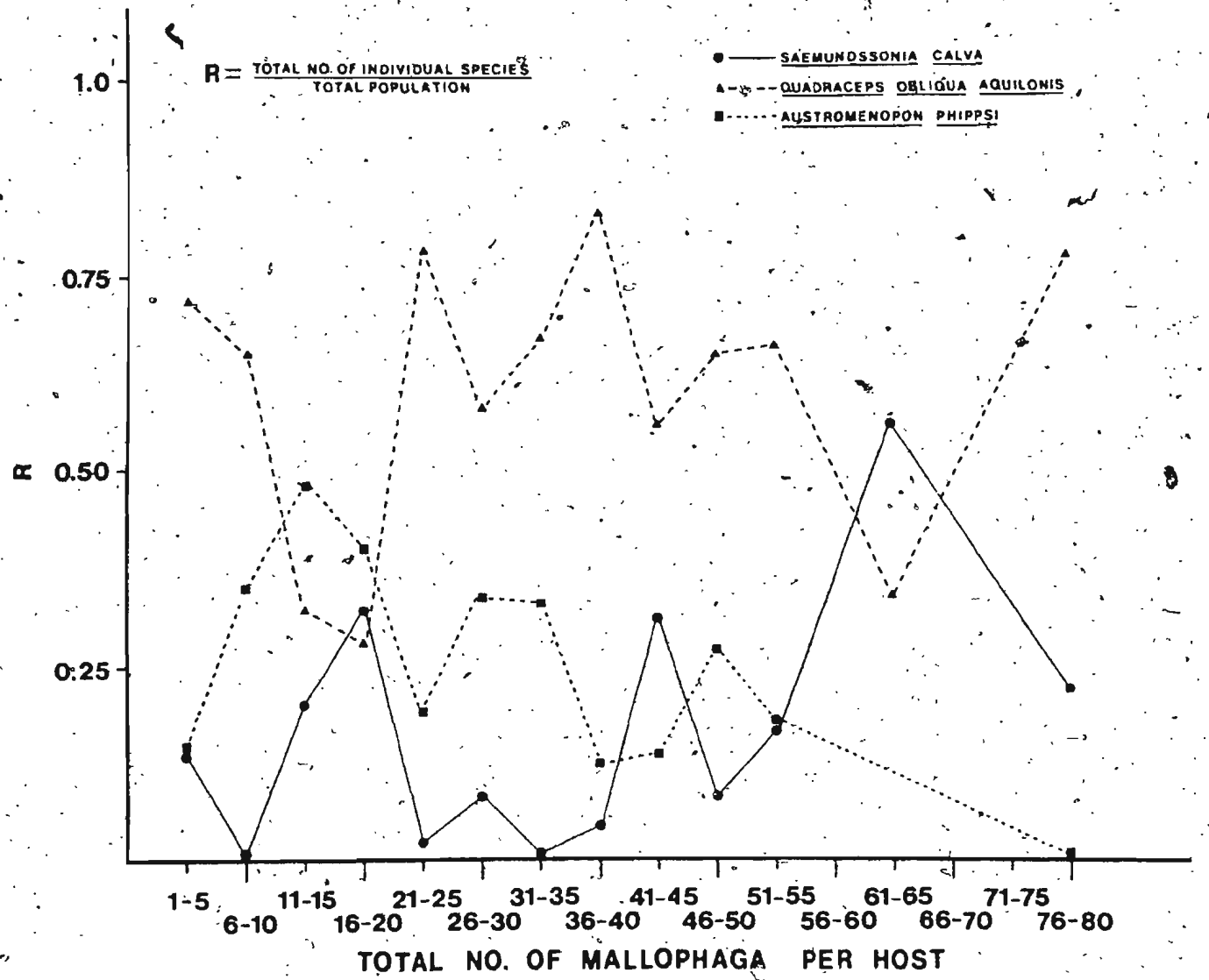

R = TOTAL NO. OF INDIVIDUAL SPECIES / TOTAL POPULATION
SAEMUNDSSONIA CALVA
QUADRACEPS OBLIQUA AQUILONIS
AUSTROMENOPON PHIPPSI
1.0
0.75
0.50
0.25
R
1-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65
66-70
71-75
76-80
TOTAL NO. OF MALLOPHAGA PER HOST

TABLE 22

DETAILS ON THE INFESTATION OF *U. LOMVIA* WITH *S. CALVA* DURING NOVEMBER AND DECEMBER, 1972

	November	December
No. Hosts examined.	32	20
Percent infested.	37.5	55.0
No. Specimens.	111	62
Mean.	9.25	5.63
Range.	1-60	1-27
No. Male specimens.	30	17
No. Male specimens per infested host.	2.50	1.54
No. Female specimens.	37	19
No. Female specimens per infested host.	3.08	1.72
No. Nymphs.	44	26
No. Nymphs per infested host.	3.67	2.36

a new geographical record for North America. A comparison of the measurements with those of Timmermann are given in Table 23.

In the present study, 88.6% of the infested hosts harboured this species, 7 hosts (15.9%) harbouring only this mallophagan. The average number per infested hosts was 11.2 (1 - 59). The frequency distribution (Fig. 10) indicates the dominance of this species on *U. lomvia*. The degree of infestation is similar to that of *Q. obliquus* on *U. aalge* but the intensity is much higher on *U. lomvia*.

All stages (except eggs) were recovered from *U. lomvia* (Table 24). The majority of specimens (91.0%) were recovered from the body regions, 40.3% being recovered from the back, 46.0% from the breast and 4.7% from the abdomen. Similar results were reported for *Q. obliquus* on *U. aalge* (Table 15). Only 0.2% were recovered from the head and 8.7% from the neck, there being little overlap with *S. calva*. In contrast to *Q. obliquus* on *U. aalge* (Table 15), no specimens were recovered from the wings and tail. No preference was shown for dorsal or ventral regions of the hosts. Nymphs represented 46.1% of the *Q. obliqua aquilonis* population, unlike *Q. obliquus* (Table 15) where only 7.3% of the population were nymphs. This unusual percentage of nymphs in a *Quadraceps* population may be the result of increased reproductive activity during the winter months. The sex ratio was 1 : 1.33 (114 m : 152 f), whereas males were

TABLE 23

MEASUREMENTS (μ) OF MALE AND FEMALE *QUADRACEPS OBLIQUUS AQUILONIS* COMPARED WITH THOSE OF TIMMERMANN, IN LITT. (MM.).

	Male								Female							
	Timmermann, in litt.				Present Study				Timmermann, in litt.				Present Study			
	Length		Width		Length		Width		Length		Width		Length		Width	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Head	0.47	0.46-0.48	0.38	0.37-0.39	482	462-494	415	395-426	0.50	0.49-0.52	0.41	0.39-0.42	506	483-520	446	426-457
Prothorax	-	-	-	-	148	145-156	275	262-286	-	-	-	-	143	140-150	275	260-286
Pterothorax	-	-	-	-	161	150-171	383	369-395	-	-	-	-	168	150-187	381	374-396
Abdomen	-	-	-	-	824	774-873	487	468-514	-	-	-	-	998	936-1029	522	504-540
Total	1.45	1.39-1.54	-	-	1570	1482-1627	-	-	1.73	1.67-1.77	-	-	1793	1716-1830	-	-
Paramere	0.12	0.11-0.14	-	-	140	135-145	-	-	-	-	-	-	-	-	-	-
C.I.*	-				0.86 (0.85-0.88)				-				0.88 (0.88-0.89)			

*Cephalic Index (width : length).

TABLE 24

DISTRIBUTION OF *QUADRACEPS OBLIQUA AQUILONIS* ON *URIA LOMVIA**

Stage		Gular	Jugu-lum	Nape	Side/ neck	Back	Breast	Abdomen
Nymph	No. hosts infested.	0	1	5	1	21	23	2
	% Total infested.	0	3.1	15.6	3.1	65.6	71.9	6.3
	Total No. in region	0	1	8	2	78	129	7
	Mean.	0	1	1.6	2	3.7	5.6	3.5
	Range.	0	1	1-2	2	1-18	1-24	3-4
	% Total *Mallophaga* in region.	0	25	26.7	22.2	39.4	57.1	30.4
Male	No. hosts infested.	0	2	6	2	22	19	1
	% Total infested.	0	6.5	19.4	6.5	71	61.3	3.2
	Total No. in region	0	2	10	4	54	40	4
	Mean.	0	1	1.7	2	2.5	2.1	4
	Range.	0	1	1-3	1-3	1-14	1-5	4
	% Total *Mallophaga* in region.	0	50	33.3	44.4	27.3	17.7	17.4
Female	No. hosts infested.	1	1	5	2	19	20	2
	% Total infested.	3.7	3.7	18.5	7.4	70.4	74.1	7.4
	Total No. in region	1	1	12	3	66	57	12
	Mean.	1	1	2.4	1.5	3.5	2.9	6
	Range.	1	1	1-4	1-2	1-17	1-12	3-9
	% Total *Mallophaga* in region.	100	25	40	33.4	33.3	25.2	52.1
Total	No. hosts infested.	1	2	7	3	30	30	2
	Total No. in region	1	4	30	9	198	226	23
	Mean.	1	2	4.3	3	6.6	7.5	11.5
	Range.	1	1-3	1-8	1-7	1-46	1-30	7-16
	% Total recovered.	0.2	0.8	6.1	1.8	40.3	4.6	4.7

*No specimens recovered from the crown, auricular, wings, tail and legs.

dominant in *Q. obliquus* on *U. aalge*.

The population structure of *Q. obliqua aquilonis* is illustrated in Fig. 12. It is evident that this species is dominant on *U. lomvia*, the population increasing steadily with increasing density. Males and females follow similar patterns throughout the population and were found to be highly correlated ($r = 0.856^{***}$, $df = 37$). Nymphs were also found to exhibit a highly significant degree of relationship with the other stages; $r = 0.807^{***}$, $df = 37$ between adults and nymphs, $r = 0.819^{***}$, $df = 37$ between females and nymphs and $r = 0.723^{***}$, $df = 37$ between males and nymphs. In contrast, no correlations existed between the various stages and sexes of *Q. obliquus* on *U. aalge*. The ratio of this species throughout the total population (Fig. 13) also indicates the dominance of this species on *U. lomvia*. With increasing population density the ratio remains relatively constant, indicating lack of competition between species at all levels of population.

The total infestation of *U. lomvia* with *Q. obliqua aquilonis* in November was higher than in December (Table 25), following the trend of the total population on these hosts. Although nymphs represented the majority of the *Q. obliqua aquilonis* population in both months, the proportion of nymphs in November was much higher than in December.

TABLE 25

DETAILS ON THE INFESTATION OF *U. LOMVIA* WITH *QUADRACEPS OBLIQUA AQUILONIS* DURING NOVEMBER AND DECEMBER, 1972

	November	December
No. hosts examined	32	20
Percent infested	81.3	65.0
No. specimens	398	93
Mean	15.3	7.2
Range	1-59	1-25
No. males	87	27
No. males per infested host	3.34	2.07
No. females	120	32
No. females per infested host	4.61	2.46
No. nymphs	191	34
No. nymphs per infested host	7.34	2.61

Austromenopon phippsi Eveleigh and Threlfall (1974)

This species was discovered in the course of the work on *U. lomvia* and is described in Eveleigh and Threlfall (1974). In the present study, 70.5% of the infested hosts harboured *A. phippsi*. The average number per infested host was 3.5 (1 - 15), slightly lower than that reported for *S. calva* on these hosts. These results are similar to those reported earlier for *A. uriae* on *U. aalge*. Only two hosts (4.5%) were found to have this species as their sole mallophagans. The frequency distribution (Fig. 10) is of the "hollow" curve type.

All stages (except eggs) were found on the hosts examined (Table 26). This is a true "body" louse, 98.7% being recovered from the back and breast (16.8% and 81.9% respectively). Unlike *A. uriae* on *U. aalge* (Table 17), only 1.4% were recovered from the head and neck. All of the specimens (0.7%) recovered from the head were from the auricular region; those on the neck (0.7%) being recovered from the side. No specimens were recovered from other body regions. Unlike *S. calva* and *Q. obliqua aquilonis*, nymphs were not the dominant stage of *A. phippsi*, representing only 26.4% of the population. This is similar to the nymph population of *A. uriae* on *U. aalge*. The sex ratio was nearly 1 : 1 (55 m : 59 f). In contrast, that of *A. uriae* on *U. aalge* was 1 : 2.11.

TABLE 26

DISTRIBUTION OF *AUSTROMENOPON PHIPPSI* ON *URIA LOMVIA* ADULTS*

Stage		Auricular	Side of neck	Back	Breast
Nymph	No. hosts infested.	0	1	7	17
	% Total infested.	0	5.6	38.9	94.4
	Total No. in region	0	1	8	32
	Mean.	0	1	1.1	1.9
	Range.	0	1	1-2	1-4
	% Total *Mallophaga* in region.	0	100	30.8	25.2
Male	No. hosts infested.	0	0	9	18
	% Total infested.	0	0	39.1	78.3
	Total No. in region	0	0	14	41
	Mean.	0	0	1.6	2.3
	Range.	0	0	1-3	1-4
	% Total *Mallophaga* in region.	0	0	53.8	32.3
Female	No. hosts infested.	1	0	4	18
	% Total infested.	4.8	0	19	85.7
	Total No. in region	1	0	4	54
	Mean.	1	0	1	3
	Range.	1	0	1	1-9
	% Total *Mallophaga* in region.	100	0	15.4	42.5
Total	No. hosts infested.	1	1	15	23
	Total No. in region	1	1	26	127
	Mean.	1	1	1.7	5.5
	Range.	1	1	1-4	1-15
	% Total recovered.	0.7	0.7	16.8	81.9

*No specimens recovered from the crown, gular, jugulum, nape, abdomen, wings, tail and legs.

The population structure of *A. phippsi* in relation to the total mallophagan population (Fig. 12) is different from the other species discussed. Numbers were highest when the total population density was average. All stages and sexes were found to be correlated, the highest correlations being found between males and females ($r = 0.667^{***}$, $df = 29$) and males and nymphs ($r = 0.553^{***}$, $df = 29$). Slightly lower correlations existed between adults and nymphs ($r = 0.519^{***}$, $df = 29$) and females and nymphs ($r = 0.435^{**}$, $df = 29$). *A. uriae* on *U. aalge* showed a reverse situation where adults and nymphs and females and nymphs had the highest correlations.

The ratio of *A. phippsi* in relation to the total population (Fig. 13) also shows that there is a decrease in this species with increasing population density. One would expect the ratio to be constant throughout the population and an explanation for this decrease could be, as mentioned earlier for *S. calva*, a reflection of few hosts with high mallophagan populations.

The infestation of *U. lomvia* with *A. phippsi* during November and December (Table 27) shows the percentage of infested hosts was less in November, but the intensity was higher than in December. A similar situation was observed for *S. calva* on this host (Table 27). In both months the sex ratio was or was nearly 1 : 1.

As noted on the other hosts examined, the three species

TABLE 27

DETAILS ON THE INFESTATION OF *URIA LONVIA* WITH *AUSTROMENOPON PHIPPSI* DURING NOVEMBER AND DECEMBER, 1972

	November	December
No. hosts examined	32	20
Percent infested	56.3	65.0
No. specimens	105	50
Mean	5.83	3.84
Range	1-15	1-8
No. males	37	18
No. males per infested host	2.05	1.38
No. females	41	18
No. females per infested host	2.27	1.38
No. nymphs	27	14
No. nymphs per infested host	1.50	1.07

of Mallophaga on hosts do not occur with equal frequency. On *U. lomvia*, 77.2% of the infested hosts harboured more than one genus of Mallophaga. Of these hosts, 43.2% harboured only 2 genera, while 34.1% harboured all three genera. The most frequent combinations were *Quadraceps obliqua aquilonis* and *Austromenopon phippsi*, both being recovered on 12 hosts (27.2%). *Quadraceps obliqua aquilonis* and *Saemundssonia calva* were the only mallophagans recovered from 5 hosts (11.3%), while *Saemundssonia calva* and *Austromenopon phippsi* were recovered from only 2 hosts (4.5%). *Quadraceps obliquus* and *A. uriae* was also found to be the most frequent combination on *U. aalge* with *S. calva* and *A. uriae* occurring less frequently.

As previously noted for *U. aalge*, only the *Quadraceps* and *Austromenopon* species were found to be significantly correlated ($r = 0.417^{***}$, df = 42) on *U. lomvia*, no significant correlations existing between *Quadraceps obliqua aquilonis* and *Saemundssonia calva* ($r = 0.147$ (N.C.), df = 42) and *Austromenopon phippsi* and *Saemundssonia calva* ($r = 0.029$ (N.C.), df = 42). Interestingly, both *Q. obliqua aquilonis* and *A. phippsi* exhibited the highest degree of overlap in the body regions. Since the correlation is positive, competition does not exist between the species, rather it appears that the populations are similarly controlled by some external factor(s) such as host preening; temperature and humidity which would certainly be equal for both species

in regions which they both occupy. Furthermore, as mentioned previously, one would not expect competition to exist between these two species, one being an ischnoceran and the other an amblyceran, with different habits.

All of the stages and sexes of the total population on *U. lomvia* showed highly significant correlations. These include adults and nymphs ($r = 0.894^{***}$, $df = 42$), males and nymphs ($r = 0.874^{***}$, $df = 42$), females and nymphs ($r = 0.864^{***}$, $df = 42$) and males and females ($r = 0.877^{***}$, $df = 42$). One would expect these correlations since all of the stages and sexes of the individual species population were related and two of the species were related. It may be speculated that the life-cycles (which are unknown) may in some way be similar on the hosts.

One adult *U. lomvia* from Green Island, Witless Bay, captured in July, was examined for ectoparasites. It was found to harbour 20 specimens, 95% of which were *Quadraceps obliqua aquilonis*. No *Saemundssonia calva* specimens were recovered.

Two *U. lomvia* chicks, only 2-3 days old (80 and 104 gms. each), examined at the same time as the above adult, both harboured Mallophaga. The average number of specimens were 4.5 (4 - 5), all of which were *Austromenopon phippsi*. Markov (1937) reported Mallophaga on *U. lomvia* chicks 1-5 days after hatching. It also appears that, as reported by Ash (1960), amblyceras are the first to transfer to chicks.

Belopolskaya (1952) and Karpovich (1970), reported the infestation of *U. lomvia* with *Ixodes uriae* in Russia, the former author noting that 42.8% of the adult hosts and 100% of the chicks were infested.

In the present study, the only adult *U. lomvia* examined during the host breeding season, when ticks are active, harboured 53 specimens of *I. uriae*, the majority (90.6%) of which were larvae. Most of the larvae (77.1%) were found on the breast, with a few specimens found on the neck, back, and legs. Nymphs were recovered only from body regions, while all the adult females were from the gular region. No ticks were found on the wings, tail and featherless areas of the legs. No ticks were recovered, from two *U. lomvia* chicks examined, nor were any recovered from the 52 adults examined during November and December when ticks are inactive.

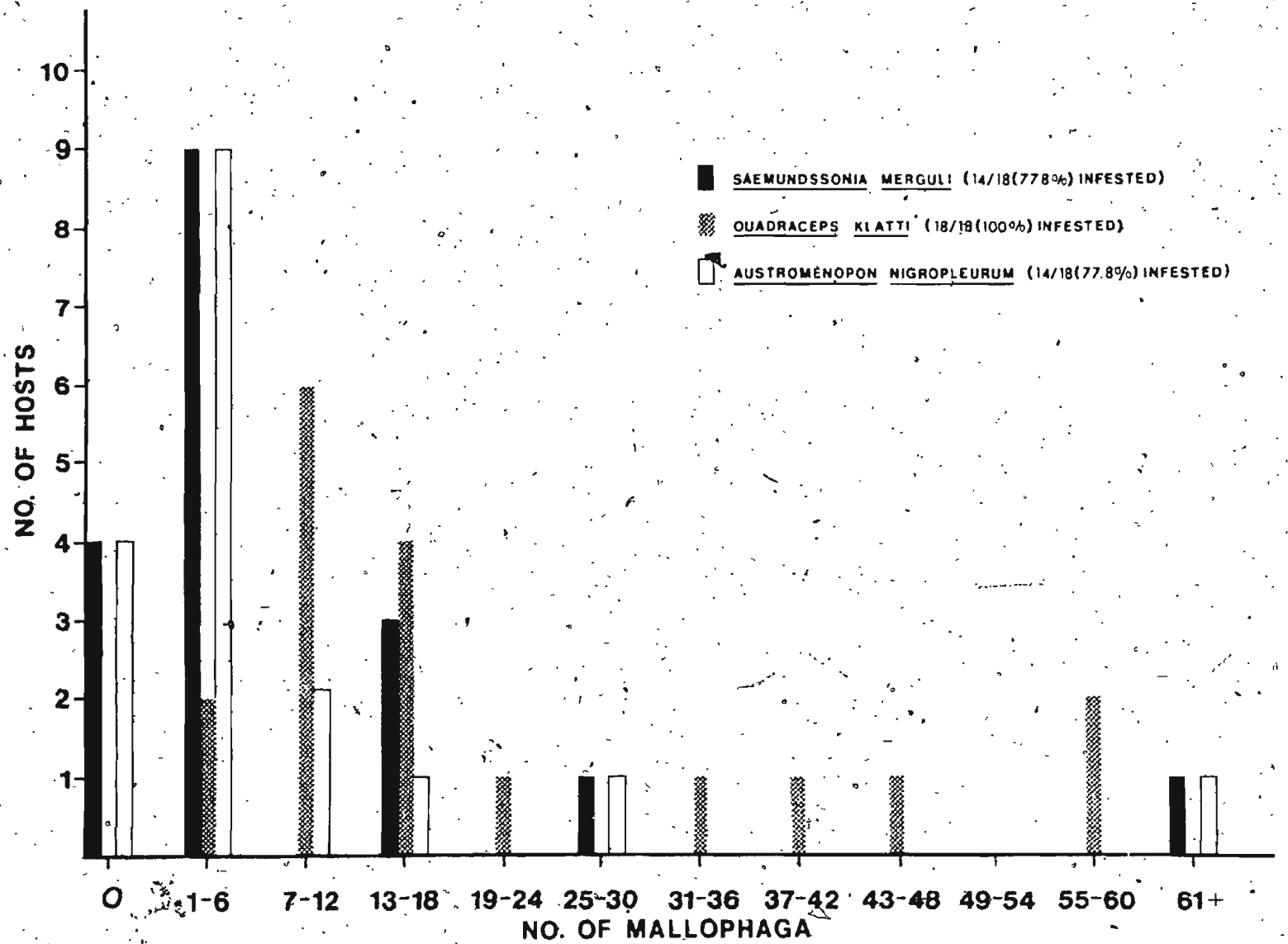
D. Dovekie (*Plautus alle* (L.))

The author is unaware of any published data on the infestation of *P. alle* with ectoparasites.

Three species of Mallophaga were recovered from the 18 adult hosts examined namely, *Saemundssonia merguli* (Denny, 1842), *Quadraceps klatti* Timmermann, 1954 and *Austromenopon nigropleurum* (Denny, 1842). All of the hosts were infested with Mallophaga; averaging 42.1 (7-191) parasites per host. The frequency distribution (Fig. 14)

FIGURE 14.

The frequency distribution of each mallophagan species on *Plautus alle*.


SAEMUNDSSONIA MERGULI (14/18(77.8%) INFESTED)
QUADRACEPS KLATTI (18/18(100%) INFESTED)
AUSTROMENOPON NIGROPLEURUM (14/18(77.8%) INFESTED)
NO. OF HOSTS
10
9
8
7
6
5
4
3
2
1
0
1-6
7-12
13-18
19-24
25-30
31-36
37-42
43-48
49-54
55-60
61+
NO. OF MALLOPHAGA

is not of the "hollow" curve type described previously, since larger numbers of parasites were present on the hosts.

No significant differences ($P > 0.05$) were found in the mallophagan burden with regard to the weight and sex of the hosts.

Saemundssonia merguli (Denny, 1842)

This species has previously been recorded from *P. alle* in Britain (Waterston, 1914) and Europe (Timmermann, 1949, 1957). Keirans (1967) reported this species from *P. alle* in New England, U.S.A., Emerson (1972) noting this record.

In the present study, 77.8% of the infested hosts harboured this species with an average of 10.7 (2 - 82) parasites per infested host. *S. merguli* was always found in mixed infestations with other mallophagans. Although this was not the dominant species on the hosts (Fig. 14), the intensity was the highest recorded for a *Saemundssonia* spp. on the alcids examined.

All stages (except eggs) were recovered from the hosts examined. The majority of specimens (84.8%) were from the head and neck regions (31.7% and 53.1% respectively) (Table 28). On the body, approximately equal numbers (7.3% and 7.8%) were recovered from the back and breast regions. No specimens were recovered elsewhere on the body.

TABLE 28

DISTRIBUTION OF *SAEMUNDSSONIA MERGULI* ON *PLAUTUS ALLE* ADULTS*

Stage		Crown	Gular	Jugulum	Nape	Back	Breast
Nymph	No. hosts infested.	3	4	1	7	3	3
	% Total infested.	25	33.3	8.3	58.3	25	25
	Total No. in region	6	11	24	24	5	4
	Mean.	2	2.8	24	3.4	1.7	1.3
	Range.	2	1-6	24	2-8	1-3	1-2
	% Total *Mallophaga* in region.	42.9	23.4	48	46.2	35.7	26.7
Male	No. hosts infested.	2	6	1	6	2	3
	% Total infested.	16.7	50	8.3	50	16.7	25
	Total No. in region	4	17	10	16	4	7
	Mean.	2	2.8	10	2.7	2	2.3
	Range.	2	1-8	10	1-4	1-3	1-5
	% Total *Mallophaga* in region.	28.6	36.2	20	30.8	28.6	46.7
Female	No. hosts infested.	3	6	1	4	3	4
	% Total infested.	30	60	10	40	30	40
	Total No. in region	4	19	16	12	5	4
	Mean.	1.3	3.2	16	3	1.7	1
	Range.	1-2	2-5	16	2-5	1-2	1
	% Total *Mallophaga* in region.	28.6	40.4	32	23.1	35.7	26.7
Total	No. hosts infested.	4	8	1	7	4	5
	Total No. in region	14	47	50	52	14	15
	Mean.	3.5	5.9	50	7.4	3.5	3
	Range.	1-6	2-19	50	3-17	1-8	1-6
	% Total recovered.	7.3	24.4	26	27.1	7.3	7.8

*No specimens recovered from the auricular, side of neck, abdomen, wings, tail and legs.

The majority (58.2%) were found on the ventral regions of the hosts. Similar to the *Saemundssonia* species on *U. aalge* and *U. lomvia*, nymphs represented 38.4% of the population. The sex ratio was nearly 1 : 1 (58 m : 60 f).

The population structure of *S. merguli* in relation to the total population on *P. alle* is illustrated in Fig. 15. It is evident that the stages and sexes follow similar patterns throughout the population. Highly significant correlations were found between males and females ($r = 0.924^{***}$, df = 12), adults and nymphs ($r = 0.961^{***}$, df = 12), females and nymphs ($r = 0.932^{***}$, df = 12) and males and nymphs ($r = 0.954^{***}$, df = 12). These correlations are similar to those recorded for *S. calva* on *Uria lomvia*. The ratio of this species in relation to the total population (Fig. 16) decreases slightly at high population densities. Again this could be the result of few hosts with high numbers of Mallophaga.

Quadraceps klatti Timmermann, 1954

This species has previously been recorded from *P. alle* in Europe (Timmermann, 1954, 1957) and New England, U.S.A. (Keirans, 1967). Emerson (1972) also recorded *Q. klatti* on *P. alle* in North America.

All of the infested birds harboured this species, the average number per infested bird being 21.1 (1 - 56) parasites. Only one host (5.6%) had this species as its

FIGURE 15

The population structure of each mallophagan species in relation to the total population on *Plautus alle*.

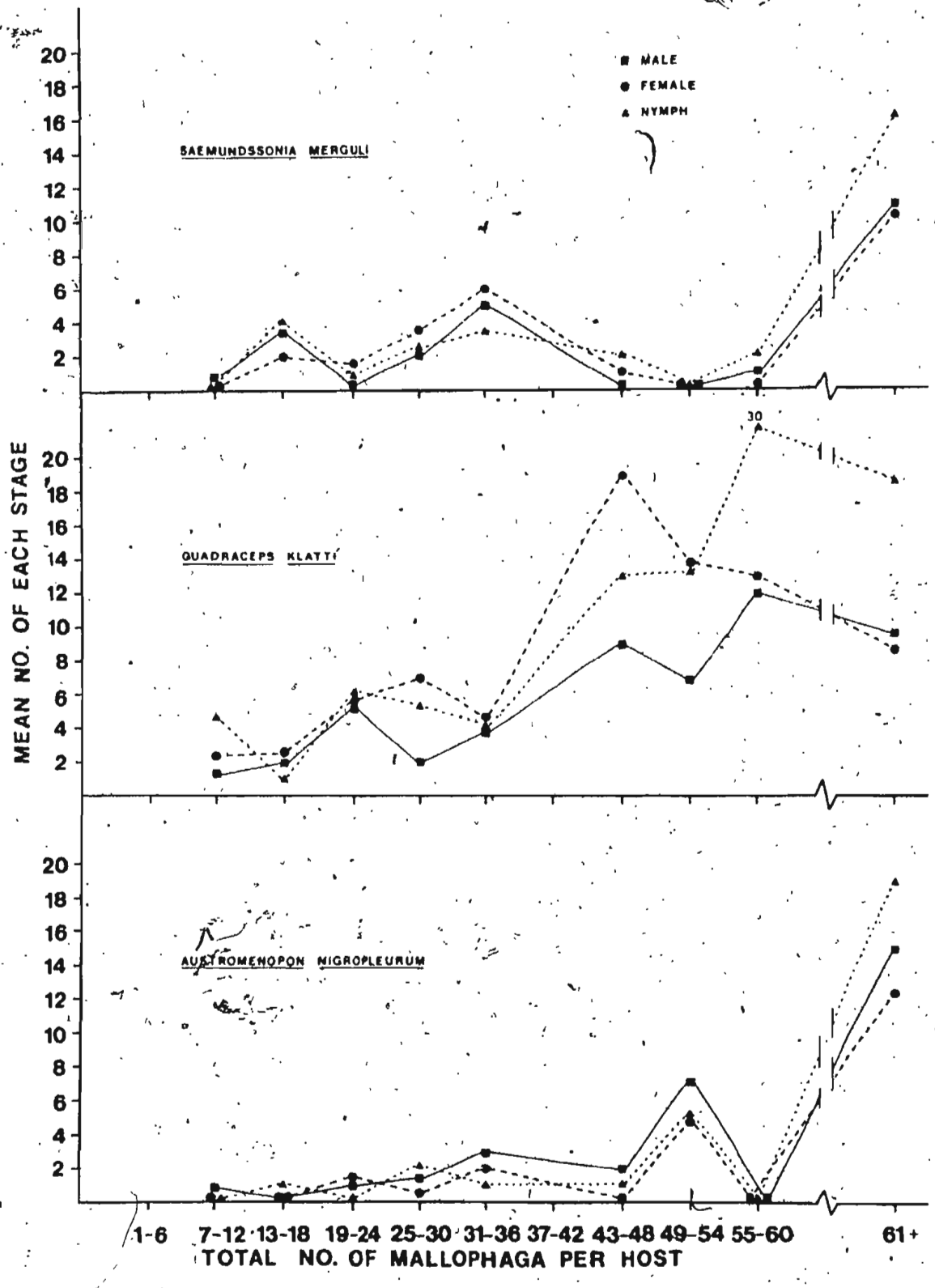
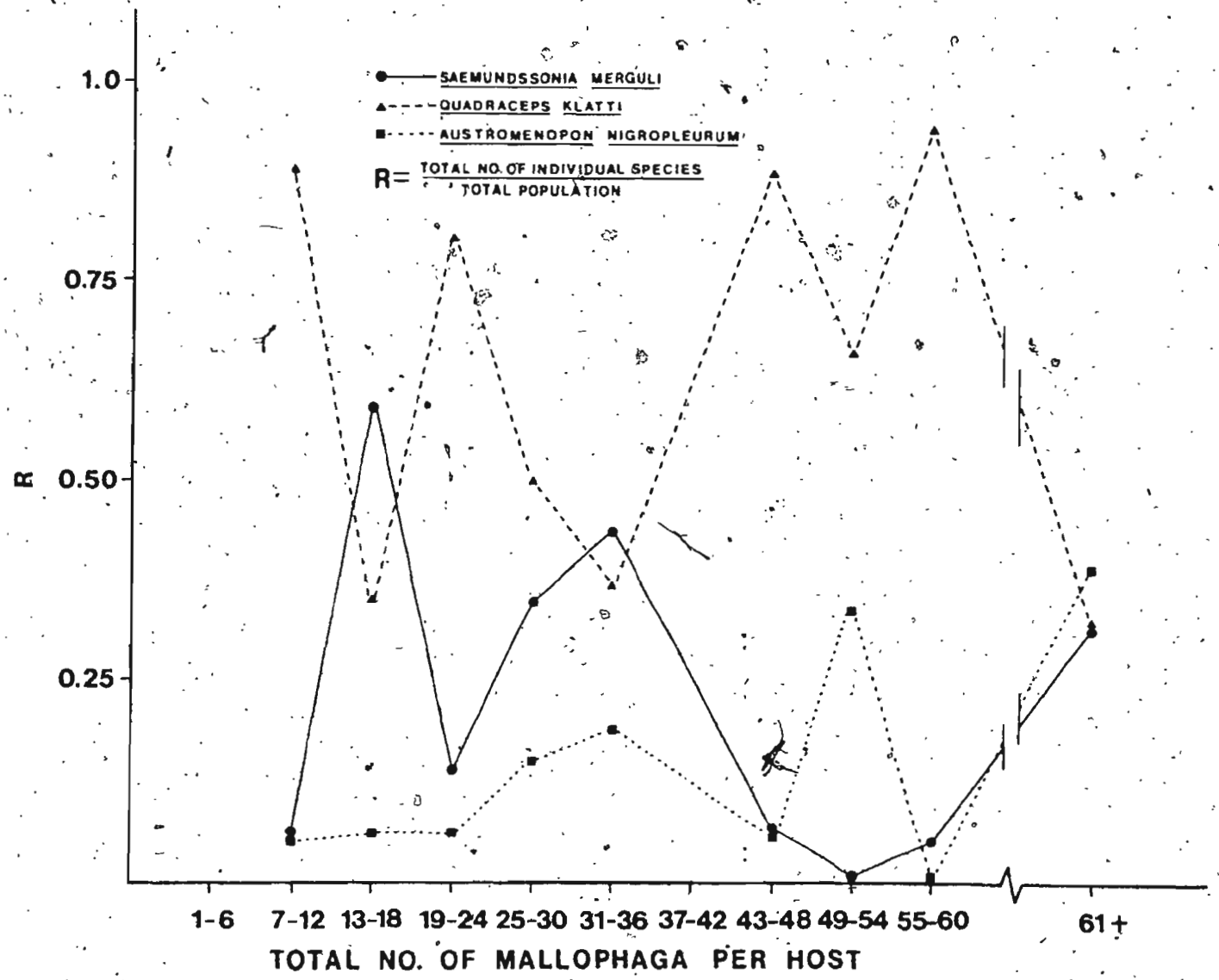

MALE
FEMALE
NYMPH
SAEMUNDSSONIA MERGULI
QUADRACEPS KLATTI
AUSTROMENOPON NIGROPLEURUM
30
MEAN NO. OF EACH STAGE
1-6
7-12
13-18
19-24
25-30
31-36
37-42
43-48
49-54
55-60
61+
TOTAL NO. OF MALLOPHAGA PER HOST

FIGURE 16

The proportion of each mallophagan species on *Plautus alle*.


SAEMUNDSSONIA MERGULI
QUADRACEPS KLATTI
AUSTROMENOPON NIGROPLEURUM
R= TOTAL NO. OF INDIVIDUAL SPECIES / TOTAL POPULATION
1.0
0.75
0.50
0.25
R
1-6
7-12
13-18
19-24
25-30
31-36
37-42
43-48
49-54
55-60
61+
TOTAL NO. OF MALLOPHAGA PER HOST

sole mallophagan. The frequency distribution of this species (Fig. 14) shows the dominance of this species on *P. alle*. This is the highest infestation of adult hosts by a single mallophagan species reported in this study.

All stages (except eggs) were recovered from the hosts examined. This was a typical *Quadraceps* species, *Q. klatti* being recovered mainly (88.2%) from the body of the hosts (28.8% and 59.4% from the back and breast respectively) (Table 29). Only 4.8% were recovered from the head; none from the auricular region. Specimens on the neck (6.9%) were recovered from the nape and side. Only one specimen (0.3%) was found on the wing primaries. No specimens were recorded elsewhere on the body. Nymphs, although not the dominant stage, represented 43.5% of the population. This is similar to *Q. obliqua aquilonis* on *U. lomvia*, thus supplementing the hypothesis that the reproductive activity of *Quadraceps* species increases during winter months. The sex ratio was 1 : 1.30 (93 m : 121 f).

The population structure (Fig. 15) also shows the dominance of *Q. klatti* on *P. alle*. The whole population increases constantly with increasing population density. It is evident that the stages and sexes are correlated, highly significant correlations being found between males and females ($r = 0.669^{***}$, df = 16), adults and nymphs ($r = 0.839^{***}$, df = 16), females and nymphs ($r = 0.742^{***}$, df = 16) and males and nymphs ($r = 0.795^{***}$, df = 16). Similar

TABLE 29.

DISTRIBUTION OF *QUADRACEPS KLATTI* ON *PLAUTUS ALLE* ADULTS*

Stage		Crown	Gular	Nape	Side of neck	Back	Breast	Wings
Nymph	No. hosts infested.	2	1	2	1	7	16	0
	% Total infested.	11.8	5.9	11.8	5.9	41.2	94.1	0
	Total No. in region	2	2	6	2	49	104	0
	Mean.	1	2	3	2	7	6.5	0
	Range.	1	2	1-5	2	1-18	2-24	0
	% Total *Mallophaga* in region.	33.3	16.7	30	33.3	45	46.2	0
Male	No. hosts infested.	2	2	5	1	8	14	0
	% Total infested.	12.5	12.5	31.3	6.3	50	87.5	0
	Total No. in region	2	4	10	3	21	53	0
	Mean.	1	2	2	3	2.6	3.8	0
	Range.	1	1-3	1-3	3	1-5	1-9	0
	% Total *Mallophaga* in region.	33.3	33.3	50	50	19.3	23.6	0
Female	No. hosts infested.	2	3	4	1	10	16	1
	% Total infested.	11.8	17.6	23.5	5.9	58.8	94.1	5.9
	Total No. in region	2	6	4	1	39	68	1
	Mean.	1	2	1	1	3.9	4.3	1
	Range.	1	1-3	1	1	1-10	1-11	1
	% Total *Mallophaga* in region.	33.3	50	20	16.7	35.8	30.2	100
Total	No. hosts infested.	4	3	6	1	12	17	1
	Total No. in region	6	12	20	6	109	225	1
	Mean.	1.5	4	3.3	6	9.1	13.2	1
	Range.	1-2	1-7	1-7	6	1-31	1-36	1
	% Total recovered.	1.6	3.2	5.3	1.6	28.8	59.4	0.3

*No specimens recovered from the auricular, jugulum, abdomen, tail and legs.

correlations were found between the stages and sexes of *Quadraceps* species found on *Fratercula arctica* and *Uria lomvia*. The ratio of this species (Fig. 16) also shows the dominance of this species in the total population. The ratio remains relatively constant with increasing population density as one would expect in a "normal" population.

Austromenopon nigropleurum (Denny, 1842)

Austromenopon merguli Timmermann, 1954 has been the species recorded from *P. alle* in Europe (Timmermann, 1954) and North America (Keirans, 1967; Emerson, 1972). Eveleigh and Threlfall (1974) regarded that this species is a synomym of *Austromenopon nigropleurum*.

A. nigropleurum was recovered from 77.8% of the infested hosts, the average number of parasites being 10.4 (1 - 28). This species was always found in mixed infestations with other mallophagans. The frequency distribution (Fig. 14) is similar to that of *S. merguli* and, in fact, the data shows remarkable similarity to that of the latter species. No comparisons can be made, however, with *A. nigropleurum* recovered from *F. arctica* because of the small numbers recorded from this host.

All stages (except eggs) were recovered from the hosts examined (Table 30). The majority of specimens (52.9%) were recovered from the head and neck (15.5% and 37.4% respectively); hence having considerable overlap with *S. merguli*

TABLE 30

DISTRIBUTION OF *AUSTROMENOPON NIGROPLEURUM* ON *PLAUTUS ALLE* ADULTS*

Stage		Crown	Gular	Jugulum	Nape	Side of neck	Back	Breast
Nymph	No. hosts infested.	1	1	1	5	1	5	6
	% Total infested.	12.5	12.5	12.5	62.5	12.5	62.5	75
	Total No. in region	6	2	16	11	1	10	25
	Mean.	6	2	16	2.2	1	2	4.2
	Range.	6	2	16	1-4	1	1-4	1-10
	% Total *Mallophaga* in region.	23.1	66.7	45.7	32.4	100	38.5	40.3
Male	No. hosts infested.	2	0	1	4	0	5	7
	% Total infested.	20	0	10	40	0	50	70
	Total No. in region	14	0	11	9	0	10	21
	Mean.	7	0	11	2.3	0	2	3
	Range.	1-13	0	11	1-4	0	1-3	1-6
	% Total *Mallophaga* in region.	53.8	0	31.4	26.5	0	38.5	33.9
Female	No. hosts infested.	1	1	1	3	0	4	5
	% Total infested.	14.3	14.3	14.3	42.9	0	57.1	71.4
	Total No. in region	6	1	8	14	0	6	16
	Mean.	6	1	8	4.7	0	1.5	3.2
	Range.	6	1	8	1-11	0	1-2	1-5
	% Total *Mallophaga* in region.	23.1	33.3	22.9	41.2	0	23.1	25.8
Total	No. hosts infested.	2	2	1	6	1	8	10
	Total No. in region	26	3	35	34	1	26	62
	Mean.	13	1.5	35	5.7	1	3.3	6.2
	Range.	1-25	1-2	35	1-19	1	1-8	1-20
	% Total recovered.	13.9	1.6	18.7	18.2	0.5	13.9	33.2

*No specimens recovered from the auricular, abdomen, wings, tail and legs.

in these regions. Of the 47.1% found on the body regions, 13.9% and 33.2% were recovered from the back and breast, respectively. No specimens were recovered elsewhere on the body. Nymphs represented 37.9% of the population, being higher than that reported for the other *Austromenopon* species discussed. The sex ratio was 1 : 0.78 (65 m : 51f).

The population structure of *A. nigropleurum* is illustrated in Fig. 15. All stages and sexes were related, highly significant correlations being found between males and females ($r = 0.979^{***}$, df = 12), adults and nymphs ($r = 0.964^{***}$, df = 12), females and nymphs ($r = 0.956^{***}$, df = 12) and males and nymphs ($r = 0.962^{***}$, df = 12). This is similar to the results reported for *A. phippsi* on *U. lomvia*. The ratio of this species in relation to the total population (Fig. 16) increases slightly with increasing population density. This may be a reflection of the small number of hosts with large numbers of Mallophaga.

The majority of hosts (94.4%) harboured more than one species of Mallophaga, all three species being found on 61.1% of the hosts. Of the hosts harbouring two species, three hosts (16.7%) harboured *Q. klatti* and *A. nigropleurum*, the same number harbouring *Q. klatti* and *S. merguli*. No hosts harboured only *S. merguli* and *A. nigropleurum*. Similar combinations were noted on the other hosts discussed.

A highly significant correlation ($r = 0.894^{***}$, df = 16) was found between *S. merguli* and *A. nigropleurum*,

no correlations existing between *Q. klatti* and *A. nigropleurum* (r = 0.019 (N.C.), df = 16) and *S. merguli* and *Q. klatti* (r = 0.158 (N.C.), df = 16). This is interesting since a correlation was always found between the *Austromenopon* and *Quadraceps* species on the other hosts examined. In this case, both *S. merguli* and *A. nigropleurum* occupied mainly the head and neck which are small areas in comparison with the body regions which *A. nigropleurum* shared with *Q. klatti*. Thus, it appears that both species must be affected by the same conditions, the correlations being positive.

As noted for the mallophagan population on other host species, the stages and sexes of the whole population on *P. alle* were related. Highly significant correlations were found between adults and nymphs (r = 0.928***, df = 16), females and nymphs (r = 0.881***, df = 16), males and nymphs (r = 0.940***, df = 16) and males and females (r = 0.929***, df = 16). Again it appears that, regardless of the relationship between the mallophagan species on hosts, the stages of the whole population are always related.

E. Black guillemot (*Cepphus grylle* (L.))

Two species of Mallophaga, namely *Saemundssonia grylle* (O. Fabricius, 1780) and *Quadraceps klatti* Timmermann, 1954), were recovered from the *C. grylle* examined. Of the 10 specimens examined during November and December, only 50%

were infested, the average number per infested host being 2.2 (1 - 6) parasites. This low infestation may be attributed to the winter molting of the hosts at this time. However, two adult hosts examined in July were parasite free.

Saemundssonia grylle (O. Fabricius, 1780)

Saemundssonia grylle has previously been recorded from *C. grylle* in Britain (Waterston, 1914) and in Europe (Timmermann, 1949, 1957). Emerson (1972) listed this species on *C. grylle* in North America.

In the present study, 60% of the infested hosts harboured this species, the average number per infested bird being 3 (1 - 6) lice. Two hosts (20%) harboured this species as their sole mallophagans. The majority of specimens were nymphs, representing 77.8% of the population. In contrast to the *Saemundssonia* species on other hosts, 55.6% of the specimens were recovered from body regions.

Quadraceps klatti Timmermann, 1954

Timmermann (in litt.) reported *Quadraceps alcae* from *Cepphus grylle* in Europe. However, the two specimens recovered from the hosts examined in the present study were *Quadraceps klatti*, this being a new host and geographical record. A comparison of the measurements of this species on *C. grylle* and *P. alle* are given in Table 31. It is possible that this is a straggler, probably from *P. alle*.

TABLE 31

MEASUREMENTS (μ) OF *QUADRACEPS KLATTI* FROM *CEPPHUS GRYLLE* AND *PLAUTUS ALLE*

	Cepphus grylle				*Plautus alle*							
	Male		Female		Male				Female			
	Length	Width	Length	Width	Length		Width		Length		Width	
					Mean	Range	Mean	Range	Mean	Range	Mean	Range
Head	410	328	458	364	421	395-437	339	322-354	454	426-468	364	348-374
Prothorax	104	218	104	244	121	114-130	230	213-234	130	124-140	245	229-255
Ptero-thorax	140	280	161	328	135	130-145	297	270-307	144	119-156	326	312-333
Abdomen	665	338	951	432	683	650-718	396	390-400	953	931-988	451	432-468
Total	1300	-	1664		1342	1274-1357	-	-	1671	1612-1732	-	-
Paramere	120	-			129	125-135	-	-	-	-	-	-
C.I.*	0.80		0.79		0.81 (0.79-0.82)				0.81 (0.80-0.82)			

*Cephalic Index (width : length).

F. Razorbill (*Alca torda* (L.))

Three species of Mallophaga, namely *Saemundssonia celidoxa* (Bermister, 1838), *Quadraceps alcae* (Denny, 1842) and *Austromenopon nigropleurum* were recovered from the hosts examined. Three out of four adult hosts examined were infested with an average number of 6 (1 - 16) parasites. Two out of four chicks examined were infested, the average number per infested chick being 5.0 (4 - 6). It is unusual for chicks to have a lower infestation than adults, although the data could be a reflection of the small numbers examined.

Saemundssonia celidoxa (Bermister, 1833)

This species has previously been recorded from *A. torda* in Britain (Waterston, 1914), Iceland (Overgaard, 1942) and in Europe (Timmermann, 1949, 1957). Emerson (1971) listed this species on *A. torda* in North America.

In the present study, two of the adults harboured this species, while only one chick was infested. All the specimens recovered were adult and from the head regions of the hosts.

Quadraceps alcae (Denny, 1842)

Timmermann (1957, in litt.) recorded this species from *Alca torda* in Europe, Emerson (1972) reporting it from *A. torda* in North America.

In the present study, only one adult host and two

chicks were infested with *Q. alcae*. All specimens were recovered from body regions of the hosts. A total of 8 males, 8 females and 8 nymphs were collected.

Austromenopon nigropleurum (Denny, 1842)

This species has been recorded from *A. torda* in Iceland (Overgaard, 1942), in Europe (Timmermann, 1954, 1957) and in North America (Emerson, 1972).

In the present study, only one *A. torda* chick harboured one female *A. nigropleurum*. None were recovered from the adult hosts examined.

Ixodes uriae has been recovered from *Alca torda* by Flint and Kostyrkc (1967) and Karpovich (1970) in Russia and by Mehl (1968) in Norway. However, no dates or details of its infestation are available from the literature.

In the present study, two of the three adults examined during the host breeding season (July) were infested with *I. uriae*. The average number of ticks per infested host was 3.5 (2 - 5). Two nymphs were recovered from the fleshy membrane between the toes of one adult host, a phenomenon noted by Bianki (1967; *vide* Karpovich, 1970) and Kaftanovsky (1951; *vide* Karpovich, 1970) for adult *A. torda*. No female ticks were recovered.

Of the four *A. torda* chicks examined, only one (approx. 4 days old) was infested with *I. uriae*. Four

nymphs were recovered from the membrane between the toes and one in the feathered area of the leg. Belopolskaya (1952) noted that ticks readily attached to the toe membranes of fledgling birds, Flint and Kostyrkc (1967) reporting that 4.1% of the ticks were recovered from the legs of *U. aalge*. One nymph was also recovered from the wing. No larva and female ticks were recovered. These were the only chicks of the alcids examined that harboured ticks. Karpovich (1970) also reported few ticks from the alcid chicks he examined.

Belopolskaya (1952) reported the infestation of adult *Alca torda* with two species of feathermites in Russia, namely *Sternosternum waterstoni* (Hirst) and *Alloptes minor* (Trouessart, 1885), noting that 95.4% were infested with the latter species. Dubinin (1952) also reported *A. minor* from *A. torda* in Russia.

In the present study, feathermites (*Alloptes minor(?)*) were recovered from 50% of the four *A. torda* chicks examined. One chick harboured approximately 150 specimens, mainly from the breast and abdomen regions, while approximately 100 specimens were recovered from the breast region of the other chick. Although the adult parent of the latter chick was examined, no feathermites were recovered, the same being noted for all the adult hosts examined.

General Discussion

No significant difference ($P > 0.05$) was found between the mallophagan populations on hosts examined during the two years of this study. Similar results were reported by Baum (1968) for the mallophagan population on blackbirds (*Turdus m. merula* (L.)) in Germany.

No significant differences ($P > 0.05$) were found in the mallophagan burden of male and female alcids examined. Similar results were reported by Touleshkov (1965) on starlings (*Sturnus vulgaris* L.) and by Foster (1969) on the Orange-crowned warbler (*Vermivora celata* (Say)). Ash (1960) noted that significantly more male chaffinches (*Fringilla coelebs* L.) were infested with Mallophaga than females, the same situation being seen in *T. merula*. Post and Enders (1970) also reported that significantly more male Seaside Sparrows (*Ammospiza maritima* (Wilson)) were infested than females.

The weight of the host had no significant effect ($P > 0.05$) on the mallophagan burden of any of the hosts except *U. lomvia*. On this host it was found that the infestation decreased significantly ($P < 0.01$) with increasing weight of the host. Judging from the range of weights (Appendix 1), it seems probable that the sample was composed of fledglings as well as adult birds. Thus, it appears that the mallophagan burden varies inversely with age of the host, becoming static as the host matures. This

hypothesis is further strengthened since the incidence of *U. lomvia* infestation remains constant during November and December while the intensity is much lower in December (Table 20). Ash (1966) reported no significant difference in the weight of uninfested and infested birds he examined.

During the breeding season of adult *F. arctica*, fluctuations occurred in their mallophagan population. These can be attributed, in most cases, to the biology of the host with which Mallophaga share a close relationship. Increased nesting activity of the host in May and early June, the hatching of chicks in July and August, and the preparation for the postnuptial molt in September could account for some of the fluctuations. Woodman and Dicke (1954) reported that the mallophagan population on the house sparrow (*Passer domesticus* L.) was highest in the spring, and speculated that this increase may have been correlated to a change in habits of the hosts during maximum breeding activity. Ash (1960) supported this hypothesis, Touleshkov (1965) adding that warmer temperatures in spring might also be a factor.

The decrease in infestation of the adult *F. arctica* in July and August may be attributed to the transfer of Mallophaga from adults-to-chicks. Foster (1969) reported decreases in the breeding of the mallophagan species of *V. celata* during egg-laying of the host, noting that the major breeding period of the Mallophaga is timed so that maximum numbers

are available for the readily accessible hosts in the nests. Ash (1960) reported, however, that the reduction in the mallophaganpopulation on adult hosts after the breeding season cannot be accounted for by transfer to nestlings, since only 28 (22.4%) of the 125 juvenile birds which he examined were infested with Mallophaga. This certainly is not the case, in the present study, where a greater percentage of the chicks were infested than adults (Table 2).

The high infestation in September may be attributed to the host postnuptial molt which commences in October, the breeding of the Mallophaga increasing to ensure survival during this molt. Baum (1968) reported that the molting of *T. merula* was the most important factor affecting the survival of their Mallophaga, Ash (1960) finding lice of the family Philopteridae attached to molted feathers picked up in the field. Foster (1969) also noted the absence of Mallophaga eggs on *V. celata* during the molt. Hence, one would speculate that there must be some survival mechanism to compensate for losses during the host molt. Another possibility is that noted by Dogel and Karolinskaya (1936 (*vide* Ash, 1960)) on the swift (*Apus apus*), where the Mallophaga increased considerably in an active state prior to the host migration. The transfer of Mallophaga from chicks-to-adults after establishment on the latter hosts is also a possibility since they transfer readily when handled (personal observations).

Foster (1969) postulated that the Mallophaga on *U. celata* especially amblycerans (partial blood feeders), have their activities controlled by host hormones. She also found that the ischnocerans (feather feeders) did not follow the life cycle as closely as the former species but did exhibit peaks of breeding coinciding with the breeding season of the majority of its hosts. It may be postulated that the population of Mallophaga (mostly ischnoceran) on *F. arctica* show similar synchronization with the life-cycle of its hosts.

The transfer of Mallophaga from adult-to-chicks occurs soon after the hatching of the chicks, lice being found on chicks 1 - 2 days old. On *F. arctica* chicks, *Quadraceps* sp. was the first to transfer, while *Austromenopon* sp. occurred first on *U. lomvia* chicks. Baum (1968) reported that the transfer of Mallophaga was influenced only by their ability to move, Ash (1960) noting that amblycerans are the first to appear on nestling birds as they are no doubt able to find food before feathers appear. Since alcid chicks hatch well covered with down, this is not entirely the case. *Saemundssonia* spp., being a slow moving louse, occurred on *F. arctica* chicks at a later age, none occurring on the *U. aalge* chicks examined.

The infestation of adult alcids with Mallophaga appears to be related to the nesting habits of the hosts. *F. arctica* being a burrow-nester with relatively little

contact with other *F. arctica* have low incidence (67.2%) and low intensity (7.3 lice per infested host) (Table 2). *A. torda* (75% infested with an average of 6 lice per infested host) and *C. grylle* (41.7% infested with an average of 2.2 lice per infested host), both being mainly crevice or boulder nesters with little contact with others of its species, showed similar results. However, *P. alle* mainly crevice-nesters were 100% infested with Mallophaga with an average of 42.1 lice per host. This high infestation could be due to their occurrence in enormous colonies in the north (Dement'ev and Gladkov, 1951; Solomonsen, 1951) with high chances for contact with others of its species on the cliffs and in the crevices. *U. aalge* and *U. lomvia*, being ledge nesters with frequent contact with each other, were highly infested (82.1% infested with an average of 10.2 lice per infested host and 84.6% infested with an average of 18.6 lice per infested host respectively). Post and Enders (1970) compared the infestation of two *Ammospiza* spp., occupying the same habitat, noting that the species occupying the wetter area of the marsh and feeding closer to the ground had a higher incidence and intensity of infestation with Mallophaga. Hence, it appears that the habits and habitat of the hosts affect the mallophagan burden of the hosts.

The incidence of mallophagan infestation on *F. arctica* chicks was much higher than that of the adults (Table 2),

while that of the *U. aalge* chicks was similar to that of the adult hosts (Table 13). In both cases, however, the intensity of infestation was much greater than that of the adult hosts. Touleshkov (1965) likewise reported that young *S. vulgaris* were more intensively infested by Mallophaga than adults. However, Baum (1968) reported that more young *T. merula* were infested than mature ones, but that the number of parasites on young birds was lower. He also stated that the incidence of Mallophaga on fledglings was less than on young and mature birds. It may be postulated that the difference in the intensity of infestation of adult and chicks could depend upon the host species and their Mallophaga.

Undoubtedly breeding by the Mallophaga occurred on the chicks, nymphs always being the dominant stage on these hosts. The only eggs recovered during the study were from laboratory reared chicks. Van Den Broek (1967) recorded eggs on chicks of the *L. ridibundus* soon after the infestation with adults. Foster (1967) reported, however, that eggs were not recovered from juvenile *V. celata*. One would consider that some survival adaptation would be necessary to compensate for losses during the molt of down feathers and that the transfer from adults-to-chicks would be in insufficient numbers if breeding did not occur on the chicks. Again this may depend upon the species of Mallophaga and the type host.

It is unlikely that the Mallophagan infestation of

alcids has any harmful effect on these hosts other than probably minor irritation, the preening activity of the hosts undoubtedly keeping their numbers to a minimum. Mallophaga can, however, be harmful if the host is in poor health or has a physical deformity, such as an abnormal bill (Ash, 1960; Nelson and Murray, 1971). In this study, one *U. aalge* chick, reared in the laboratory, became heavily infested with *Austromenopon uriae*. The bird gradually lost condition and eventually died, partly through the influence of this parasite which undoubtedly is wholly or partially dependent on blood like other amblycerans (Ash, 1960; Kalamarz, 1963a, b).

Saemundssonia spp. were found on all species of alcids examined. These ischnocerans were generally found on the ventral surfaces of the feathers; the adults usually resting on the feathers with their mouthparts firmly around the barbules, the nymphs being more active, usually seen running through the feathers or over the skin. All species fed solely on pieces of feathers.

On adult *F. arctica*, *Saemundssonia* was the dominant genus (Fig. 6), 96.4% of the infested hosts harbouring this genus with an average of 5.4 lice per infested host. The monthly infestation of these hosts with this genus (Table 6) closely followed that of the total population (Table 3). On adults of the other alcid species, with the exception of *P. alle* where the incidence was 77.8% with a high intensity of 10.7 lice per infested host, the incidence and intensity

of infestation with this genus was low; being 56.5% and 1.9 for *U. aalge*; 52.3% and 3.9 for *U. lomvia*; 60% and 3.0 for *C. grylle*; 66.6% (2 of 3) and 0.7 for the *A. torda*. These differences in the infestation of the various host species could be due to genetic differences in the *Saemundssonia* species on each host species as well as host differences. The similarity in the infestation of *U. aalge* and *U. lomvia* reflects this hypothesis since both hosts are genetically similar and infested with the same *Saemundssonia* species--*S. calva*.

In contrast to the situation on adult alcids, only 50% of the infested *F. arctica* chicks harboured specimens of *Saemundssonia* with an average of 4.7 lice per infested host. Despite this difference in incidence, the intensity was similar to that on adults. *U. aalge* and *U. lomvia* however, harboured no specimens of this genus with only 50% (1 of 2) *A. torda* chicks being infested with 1 specimen. This could be a reflection of small sample size or, as mentioned earlier, the result of a later transfer of this genus to these chicks.

Saemundssonia can be accurately termed "head" lice since, on all the alcid species examined, the majority occupied the head and neck. However, depending upon the host species, the percentage of specimens which occupied the head and the neck varied; 60.4% on the head and 37.7% on the neck of adult *F. arctica*; 57.8% and 35.6% on adult

U. aalge; 1.2% and 88.3% on adult *U. lomvia*; 31.7% and 53.1% on adult *P. alle*. The data on *C. grylle* and *A. torda* are not included due to low numbers recorded. It may be speculated that the majority of specimens occupying the necks of *U. lomvia* and *P. alle*, as opposed to *F. arctica* and *U. aalge*, is in response to lower temperatures on the head during the colder winter months, the species moving to the neck where undoubtedly the temperature would be higher due to denser plumage. The *Saemundssonia* species on *F. arctica* and *P. alle* showed definite preference for ventral body regions, whereas the species (*S. calva*) on *U. aalge* and *U. lomvia* showed preferences for dorsal body regions. This could be due to differences in the biology of the particular louse species. No specimens were found on the abdomen, legs, and tail of all the host species.

Although no *Saemundssonia* specimens were found on *U. aalge* and *U. lomvia* chicks, those recovered on *F. arctica* showed a similar distribution to those on adults with the exception that on the head the majority preferred the auricular region and dorsal body regions in general.

Nymphs were not the dominant age class of *Saemundssonia*, the percentage being similar on all adult host species. On *F. arctica*, nymphs were highest in spring and fall, an indication of increased reproductive activity during these times. As discussed earlier, nymphs were dominant on *F. arctica* chicks.

The sex ratio was similar on *F. arctica* and *U. aalge* (1 : 0.81 and 1 : 0.73 respectively); however, on *U. lomvia* and *P. alle* females were more common (1 : 1.19 and 1 : 1 respectively). Whether females are more common in a population during winter months is not known but the difference in the ratios of the species (*S. calva*) on *U. aalge* and *U. lomvia* appears to reflect this. This could also be a reflection of different population structures on different hosts due to host influences on their biology. The sex ratio on *F. arctica* chicks was 1 : 1, the population being reproductively active, as discussed previously.

The population structure of *Saemundssonia* varied with the host species. The males and females were highly significantly correlated on all hosts except *U. aalge* from which low numbers were recovered. One would expect such a correlation to exist in a "normal" population but, as noted by Buxton (1941) for the human head-louse, these high correlations would not be expected, considering the inequality of the sexes on certain hosts. Significant correlations were found between the stages and sexes of the *Saemundssonia* populations only on *U. lomvia* and *P. alle*. This lack of correlation on *F. arctica* cannot be explained at present, but on *U. aalge* may be due to low numbers recovered. On all host species, the density of the total Mallophagan population had no significant effect on the ratio of *Saemundssonia* present on hosts. Thus, it appears that

little interaction with other species occurs on the hosts, even at high population densities, and the species may be viewed as a separate spatial entity on the hosts.

Similar to *Saemundssonia*, *Quadraceps* spp. were found on all the alcid species examined. These ischnocerans are long and slender enabling them to lie between the barbs of the feathers to avoid preening. This adaptation, coupled with their greater mobility, has enabled them to occupy a wider variety of habitats on the hosts. The examination of crops revealed that this is likewise a feather feeder.

Quadraceps was the dominant genus on adult *U. lomvia* and *P. alle* with an incidence and intensity of 88.6% and 11.2, and 100% and 21.1, respectively. On adult *U. aalge*, the genus was not entirely dominant, having the same frequency as that of *Austromenopon*, and an incidence of 86.9% and an intensity of 4.7. In contrast, *Quadraceps* on adult *F. arctica* had only an incidence of 19% and an intensity of 1.9. The data on *C. grylle* and *A. torda* are not included due to low numbers recovered. The similarity in the incidence of *Quadraceps* on adults of *U. aalge* and *U. lomvia* is interesting because both the host and the parasite are closely related. As mentioned previously, it appears that the degree of infestation of a host depends upon the biology of the particular parasite and its host species.

From the previous discussion on the transfer of Mallophaga from adults-to-chicks and the habits of *Quadraceps*,

it would be expected that the infestation of chicks with this genus would be great. Despite the low infestation of adult *F. arctica* with this genus, 91.7% of the infested chicks harboured this parasite with an average of 30 lice per infested host. Similarly, 100% of the *U. aalge* chicks harboured *Quadraceps* with an average of 20 lice per infested host. No *U. lomvia* chicks harboured this genus but this could be a reflection of the small number of hosts examined. Hence, it appears that *Quadraceps* establishes itself as a dominant genus on chicks regardless of the extent of infestation on adults. This is further support for the hypothesis that breeding by the louse species must occur on the chicks.

Quadraceps first occurred on adult *F. arctica* the last week of June, 1973 and first week of July, 1972. Touleshkov (1965) and Baum (1968) both reported species of Mallophaga on the birds they examined only in certain months. It may be postulated that, as reported by Boyd (1951) and Arora and Chopra (1959) for other species, it overwinters in the egg stage, hatching in time for the transfer to chicks in July. Few specimens were recovered from adult *F. arctica* examined in winter, further evidence for this postulation. Furthermore, the number of nymphs per infested host increased monthly, indicating that breeding must have occurred previously. The monthly infestation (Table 10), like that of *Saemundssonia*, closely followed the trend of

the total population (Table 3).

As previously mentioned, *Quadraceps* was the first to transfer to *F. arctica* chicks, being the only species present on these birds between hatching and 191 gms. in weight. Although the incidence on chicks decreased monthly, the intensity increased (Table 10). Simultaneously, both the incidence and intensity of *Saemundssonia* infestation increased. Thus, it appears that the latter species will again be dominant in spring.

Quadraceps is a true "body" louse, the majority being found on the back, breast and abdomen of all the alcids. On adult *U. aalge*, *U. lomvia* and *P. alle* the percentage occupying these regions was 87.1%, 91.0% and 88.2%, respectively. On adult *F. arctica*, however, only 58.9% occupied these regions with 34.3% occupying the neck. Thus, only on adult *F. arctica* was there any extensive overlap with *Saemundssonia* on the hosts. No distinct preference was shown for either dorsal or ventral regions of *U. aalge* and *U. lomvia*. On *F. arctica* a preference was shown for dorsal regions, while on *P. alle*, a ventral preference was shown. Again it appears that these factors depend upon the habits of the particular louse species. No specimens were found on the legs of any of the host species.

A distinct preference for the body regions of the hosts was also shown on chicks of *F. arctica* and *U. aalge* (93.2% and 73% respectively). As on adult *F. arctica*, a

preference was shown for the dorsal regions of the chicks. No preference for either dorsal or ventral regions was shown on *U. aalge* chicks.

Nymphs represented only 11.4% and 7.3% of the *Quadraceps* population on adult *F. arctica* and adult *U. aalge* respectively. In contrast, on adult *U. lomvia* and *P. alle*, nymphs represented 46.1% and 43.5% respectively of the total population. It may be postulated that increased breeding activity occurs in early winter or that eggs are laid prior to this time, the nymphs hatching throughout the winter. On adult *F. arctica* unlike *Saemundssonia*, the nymphs of *Quadraceps* increased monthly, being highest in September.

Nymphs represented 64.9% of the *Quadraceps* population on *F. arctica* chicks. On *U. aalge* chicks, however, only 31% of the population were nymphs. It is obvious that increased reproductive activity occurs on immature hosts.

The sex ratio of *Quadraceps* on adult *F. arctica* and *U. aalge* was 1 : 1 and 1 : 0.84 respectively. On adult *U. lomvia* and *P. alle*, however, the females were more common, the sex ratios being 1 : 1.33 and 1 : 1.30, respectively. Similar to *Saeumundssonia* on these latter hosts, it appears that females are the dominant sex in winter.

The sex ratio on chicks of *F. arctica* and *U. aalge* (1 : 1.28 and 1 : 1.47 respectively) was similar to that found on adult *U. lomvia* and *P. alle*, the females being the dominant sex. Again it appears that this is typical of

reproductively active populations.

The population structure of *Quadraceps*, like that of *Saemundssonia*, varied with the host species. On all hosts, the males and females were highly significantly correlated ($P < 0.001$). Only on *U. aalge* was there no correlation between the stages and sexes and this could be due to low numbers of nymphs recovered from this host. Similar to *Saemundssonia*, the ratio of *Quadraceps* remained relatively constant on all of the alcids regardless of the total population density. Thus, little influence is exerted on this population by other species.

Austromenopon spp. were recovered from all the alcids except *C. grylle*. These active amblycerans are found mainly on the host skin or running through and over the feathers. Those on *U. aalge* were observed to frequent the eyelids of the host, probably to obtain liquid eye secretions. Like *Quadraceps*, their mobility enables them to occupy a wide variety of habitats on their hosts. The crops of most amblycerans were red, undoubtedly due to ingested blood cells. As reported by Ash (1960) the amblycera are mostly dependent on blood as food.

Austromenopon was not the dominant genus on any of the alcids examined. Few specimens were recovered from adult *F. arctica*, occurring on only 4.8% of the infested hosts with an average of 1 per infested host. These were probably stragglers from other hosts (e.g. *A. torda*) on

the colony; however, two adult *F. arctica* (probably from a different population), examined in December, harboured mainly *Austromenopon* (67.1% of the total population) this being probably typical of that population. On *U. aalge*, as previously mentioned, *Austromenopon* occurred with the same frequency as *Quadraceps* but the intensity of infestation was slightly lower, being 3.5 per infested bird as opposed to 4.7 for *Quadraceps*. 70.5% of the infested *U. lomvia* harboured this genus with an average of 3.5 lice per infested bird. The *Austromenopon* infestation on *P. alle* was similar to *Saemundssonia*, 77.8% of the infested hosts harbouring this genus with an average of 10.4 per infested bird. Data on *C. grylle* and *A. torda* are not included due to low numbers recovered. As previously mentioned, the extent of infestation of a host depends upon the biology of the parasite and the host.

No *F. arctica* chicks harboured *Austromenopon*. In contrast, all the infested *U. aalge* and *U. lomvia* chicks harboured this genus with an intensity of 15.8 and 4.5 per infested bird respectively. As previously mentioned, *Austromenopon*, if present on adult hosts, is the first to transfer to the chicks, being extremely mobile and not dependent on feathers as a diet.

Austromenopon, unlike *Saemundssonia* and *Quadraceps*, did not exhibit such a well defined distribution on all the alcids. On adult *U. aalge* and *U. lomvia*, the majority were

recovered from the body (71.3% and 98.7% respectively). On *P. alle* however, the majority (52.9%) were recovered from the head and neck. Hence, on adult *U. aalge* and *U. lomvia* considerable overlap occurred with *Quadraceps*, while on *P. alle* most of the overlap was with *Saemundssonia*. On all the alcids, a definite preference was shown for the ventral regions of the hosts. No specimens were recovered from the abdomen, wings, legs and tail of any of the hosts.

Similar to the situation on *P. alle*, *Austromenopon* on *U. aalge* chicks were recovered mainly from the head and neck (51.9%). In contrast to adult hosts, a distinct preference was shown for the dorsal regions. Similar to that of *Saemundssonia* and *Quadraceps*, nymphs were not the dominant age class of the *Austromenopon* spp. on adult alcids. On adult *U. aalge* and *U. lomvia*, nymphs represented only 27.5% and 26.4% of the population respectively. On *P. alle*, nymphs were slightly higher, representing 37.9% of the population. It appears that, unlike *Saemundssonia* and *Quadraceps* little increase in the nymph population of *Austromenopon* occurs in winter. On *U. aalge* chicks, however, nymphs represented 51.8% of the population, indicating that, as previously stated, reproductive activity must occur on immature hosts.

The sex ratio of *Austromenopon* varied considerably with each host species. On adult *U. aalge*, the sex ratio was 1 : 2.11, while on adult *U. lomvia* it was 1 : 1. Females

were less common on *P. alle*, the sex ratio being 1 : 0.78. These different ratios can only be attributed to differences in the biology of each louse species. This marks the first time that females were not dominant in winter. The females were also dominant on *U. aalge* chicks, the sex ratio being 1 : 1.38.

The population structure of *Austromenopon*, as previously noted for *Saemundssonia* and *Quadraceps*, varied with the host species. On all the hosts, significant correlations were found between males and females. Significant correlations also existed between the stages and sexes on all the hosts except *U. aalge* where no correlation was found between males and nymphs and, as mentioned earlier, this could be due to the low number of nymphs in the population. Similar to *Saemundssonia* and *Quadraceps*, the ratio of this species remained relatively constant on all the hosts at all population levels. Despite its overlap with the other two genera, there appears to be no effect on the population.

Highly significant correlations ($P < 0.001$) were found between *Quadraceps* and *Austromenopon* on *U. aalge* and *U. lomvia* and between *Saemundssonia* and *Austromenopon* on *P. alle*. On the former two hosts, *Quadraceps* and *Austromenopon* shared basically the same habitat on the hosts and consequently were affected by the same environmental conditions offered by the habitat. The same is true on *P. alle* where

Saemundssonia and *Austromenopon* occupied basically the same habitat. The correlations, being positive, suggest that competition does not occur between the genera. Rothschild and Clay (1961) suggested that interspecific competition may be a factor limiting population size; however, in this study, no competition was noted on any of the hosts, since with increasing population density, the ratio of each individual species remained relatively constant. On the basis of what is known about each genus, one would not expect interspecific competition to occur, since the greatest overlap always occurred between an ischnoceran and an amblyceran, whose diets are completely different. Whether there is intraspecific competition is not known, but some species are known to be cannibalistic (Rothschild and Clay, 1961; Nelson and Murray, 1971).

All the stages and sexes of the total mallophagan population on all the adult alcids were found to be significantly correlated, regardless of whether the stages and sexes of a particular species or the different species on a host were related. It appears that the life-cycles of the various species must be similar or, failing this, must be similarly affected by some external factor so that only a certain number of each stage and sex occurs on hosts. So little is known of the life-cycles of mallophagan species that definite conclusions cannot be drawn.

In the present study, some hosts harboured species

characteristic of another host, suggesting that straggling sometimes does occur. Waterston (1914) recorded that each species of British auk has its own characteristic species of Mallophaga, but three of the bird species examined harboured Mallophaga that were characteristic of another auk species. He noted that the birds concerned, *F. arctica*, *A. torda* and *U. aalge* were species that have the greatest chance of consort with one another on cliffs. Undoubtedly this accounts for similar species occurring on certain hosts in the present study, for example, *Saemundssonia calva* on both *U. aalge* and *U. lomvia*.

The distribution of Mallophaga on seabirds provide excellent material for a study of changes in parasitic fauna (Dogiel, 1963), and the population dynamics of these parasites. Until more is known about the life-cycle and bionomics of Mallophaga, however, the interpretation of data often can only be postulated. One cannot overstress the need for more work in this area.

No significant difference ($P > 0.05$) was found in the *Ixodes uriae* burden on adult alcids with regard to sex and weight of the hosts.

While no significant difference ($P > 0.05$) was found in the infestation of adult *U. aalge* in 1972 and 1973, the infestation of adult *F. arctica* was considerably higher in 1973 than 1972 (Table 11). This could be due to a mass die-off of immature *L. argentatus* (Threlfall *et al.*, 1974),

a common host of *I. uriae*, thus making *F. arctica* more frequented hosts. Flint and Kostyukc (1967) reported a similar situation in Russia, where the infestation on *Rissa tridactyla* greatly increased when *U. aalge* were scarce due to lack of food.

The incidence of *I. uriae* on *U. aalge* was much higher than that on *F. arctica*, being 65.2% and 18.4% respectively. The average number per infested bird, however, was considerably higher on *F. arctica* (15.6) than on *U. aalge* (4.5). Undoubtedly this is due to more *U. aalge* being readily accessible in the colony. The data on *U. lomvia* and *A. torda* is insufficient for comparative purposes.

The distribution of *I. uriae* on *F. arctica* was somewhat different than that on *U. aalge*. Only 9.3% of the ticks were recovered from the head and neck of *F. arctica*, while 43.3% were recovered from these regions on *U. aalge*. No preference was shown for dorsal and ventral regions of the hosts. Ticks were recovered from the fleshy membrane between the toes of only one adult *A. torda*.

Female ticks were recovered only from the neck of the hosts, while nymphs were recovered mainly from the head and neck of *U. aalge* (90%) and mainly from the body of *F. arctica* (69.6%). On both hosts, larvae were recovered mainly from the body regions (63.7% on *U. aalge* and 92.1% on *F. arctica*).

The population structure was also different on *F. arctica* and *U. aalge*. Larvae represented 85.4% of the

population on *F. arctica* but only 47.7% on *U. aalge*. Only 12.8% of the population were nymphs on *F. arctica* whereas 44.7% were nymphs on *U. aalge*. On both hosts, females represented only a small percentage of the population, being 7.4% on *U. aalge* and 1.7% on *F. arctica*. Undoubtedly, these differences in infestation and distribution on *F. arctica* and *U. aalge* is due to differences in the biology of the hosts.

Ticks were recovered from only one *A. torda* chick in this study. It appears that immature alcids play a minor role in the tick life-cycle although Flint and Kostyrko (1967) and Karpovich (1970) reported that fledglings play a major role as hosts during the second half of the summer in Russia.

On none of the hosts did the presence of *Ixodes uriae* adversely affect the Mallophaga population of these hosts as was reported by Waterston (1914) on British auks.

Feathermites of the genus *Alloptes* were recovered from adult *F. arctica* and *A. torda* chicks. While only two specimens were recovered from adult *F. arctica*, large numbers were recovered from two of the four *A. torda* chicks examined. No feathermites, however, were found on adult *A. torda* although the adult parent of one of the chicks was examined.

Summary

1. The mallophagan, tick and feathermite infestation of six species of alcids namely, *Alca torda, Uria aalge, Uria lomvia, Plautus alle, Cepphus grylle, Fratercula arctica* is reported.

2. No significant differences ($P > 0.05$) were found in the mallophagan populations on hosts from year to year and with the sex of the hosts. The weight of the hosts also had no effect on the mallophagan burden of any host, except *U. lomvia* where a significant correlation ($P < 0.005$) existed. The regression equation is given showing that the infestation decreases with increasing weight.

3. No significant difference ($P > 0.05$) was found in the tick infestation of hosts with regard to sex and weight. Although no significant difference ($P > 0.05$) existed in the infestation of *U. aalge* from year to year, the infestation was much greater on *F. arctica* in 1973 than 1972.

4. Fluctuations occurred in the mallophagan population on adult *F. arctica* during the breeding season, these being related to the biology of the host.

5. The tick population on *F. arctica* showed monthly fluctuations, these being related to the life-cycle of the tick.

6. The transfer of Mallophaga from adult-to-chick occurred soon after hatching with the most active species transferring

first. Certain species were only found on chicks of a certain weight.

7. The extent of infestation of the adult alcids with Mallophaga and ticks can, in some way, be attributed to the nesting habits of the hosts, those having the greatest amount of contact being more heavily infested.

8. The intensity of infestation of Mallophaga on alcid chicks was always greater than that on the adults with certain species, which occurred infrequently on adults, being dominant on chicks. Ticks were found on only one alcid chick; feathermites infesting mainly *A. torda* chicks.

9. *Saemundssonia* spp., "head" lice, were the dominant species on only adult *F. arctica*, although it occurred on all the hosts. This species occurred only on *F. arctica* and *A. torda* chicks.

10. In summer, *Saemundssonia* occupied mainly the head regions of the hosts, but in winter moved down the neck where temperatures were undoubtedly higher. On different hosts, this species preferred certain regions, probably related to the habits of the particular species.

11. *Quadraceps* spp., are true "body" lice, being found on all the adult alcids examined. On *U. lomvia* and *P. alle* it was the dominant genus, while on *U. aalge* it occurred with the same frequency as *Austromenopon*. Few adult *F. arctica* were infested with this genus. All chicks except those of *U. lomvia* harboured *Quadraceps*. On each host the species preferred certain body regions.

12. *Austromenopon* spp., another "body" louse, occurred on all alcids except *C. grylle*. It was not the dominant genus on any of the adult hosts although all the infested *U. aalge* and *U. lomvia* chicks harboured this parasite. Unlike the other two genera, its distribution on the hosts was not well defined.

13. Nymphs were not the dominant age class of any of the species on adult hosts, although nymphal *Quadraceps* were higher in winter on *U. lomvia* and *P. alle*. In contrast, on the majority of chicks, nymphs dominated the population.

14. The sex ratio of each species varied with the host, females being generally higher on hosts in winter and on immature hosts.

15. On the majority of hosts, males and females were significantly correlated. Correlations between the stages and sexes depended upon the mallophagan species and the host.

16. The greatest overlap in habitats occupied by two genera always occurred between an ischnoceran and an amblyceran, statistically significant correlations ($P < 0.001$) always occurring between them. No competition existed between these genera since both have entirely different food habits.

17. The stages and sexes of the whole mallophagan population on hosts were always significantly correlated.

18. Similarities in most details of the mallophagan infestation of *U. aalge* and *U. lomvia* existed, suggesting that

similarities in the hosts general biology is reflected in its infestation.

19. Mallophaga were observed to have no harmful affects on wild birds although one laboratory-reared *U. aalge* chick, heavily infested with an *Austromenopon* sp., died, undoubtedly aided by the infestation. Although no visible effects were noticed in birds infested with ticks, the bites of these parasites are painful. Feathermites also had no visible effects on the hosts.

20. No differences in the Mallophaga infestation of alcids was observed due to the presence of ticks on the hosts.

21. The distribution and population structure of ticks varied with the host species. Females were always found on the neck regions of the hosts with larvae localizing mainly the body regions. Nymphs, however, showed no preference for any particular region.

PART II

BIOLOGY OF *IXODES (CERATIXODES) URIAE* WHITE, 1852

Introduction

The taxonomic position of *Ixodes uriae* has been the subject of much controversy, some workers giving *Ceratixodes* generic status, while Clifford *et al.* (1973) refer it to a subgenus of *Ixodes*, a move followed in the present study.

This so-called "puffin tick" is a common parasite of seabirds in many parts of the northern and southern hemisphere (Main, 1972). Published information on the biology of this tick is very scanty and has, for the most part, been deduced from fragmentary data, the major studies being those of Nuttall (1913), Flint and Kostyrkc (1967), Murray and Vestjens (1967) and Korpovich (1970).

The availability of both a large seabird colony and the facilities to maintain seabirds in captivity provided the opportunity to study the life cycle and biology of this tick in greater depth than previously and this part of the thesis summarizes these studies.

Materials and Methods

To determine the habitat preferences, seasonal activity and to correlate abundance of *Ixodes uriae* with host nesting

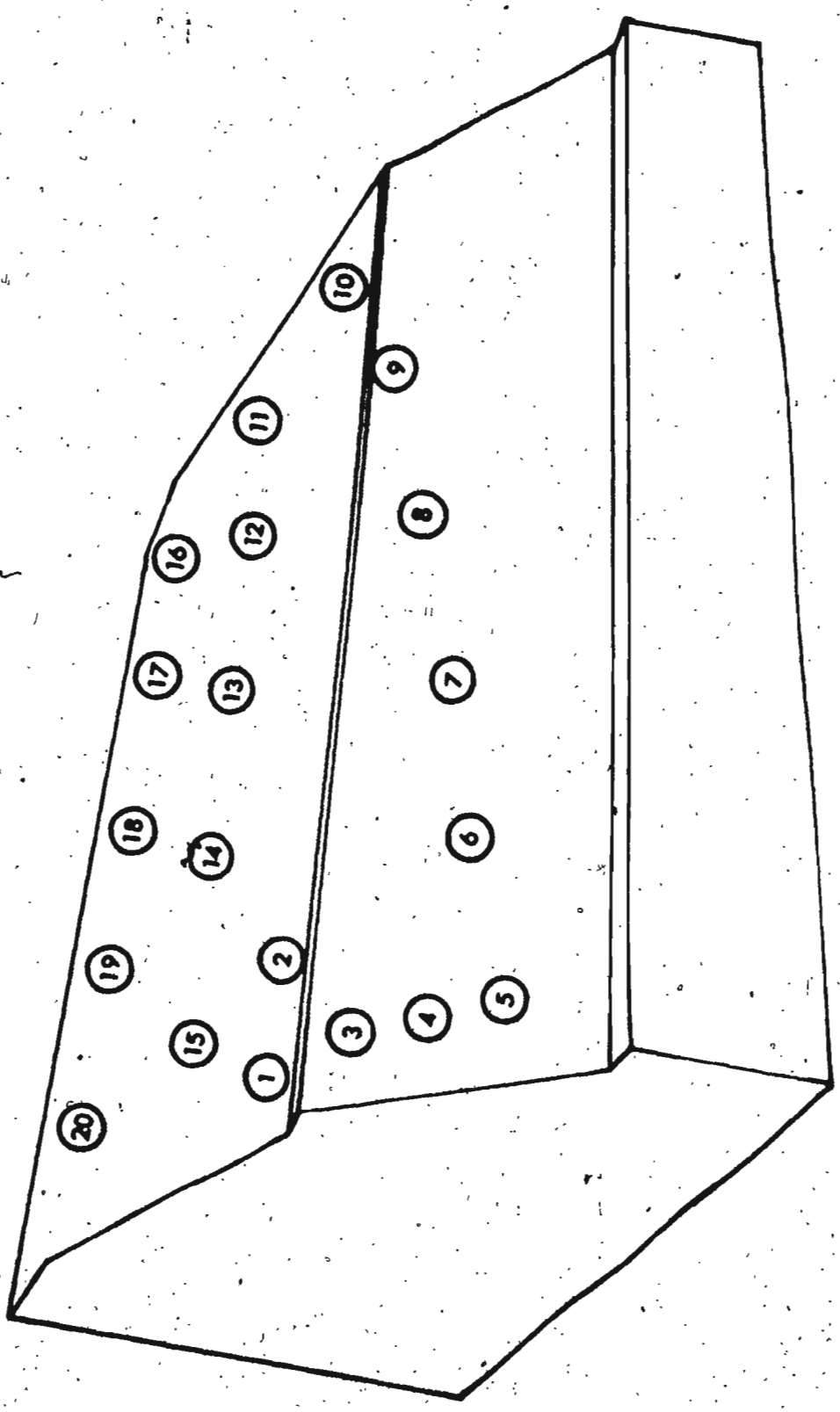
densities, 20 groups of *F. arctica* burrows (each consisting of 3 - 4 burrows) were marked, with a numbered wooden peg, on a steep slope leading from a seaward-facing cliff to the flat top of the island (Fig. 17). Soil and litter samples of approximately 700 gm. each were removed from these burrows and taken back to the laboratory where they were examined immediately, on in the event of a delay, stored in a refrigerated incubator at a temperature equal to that at which the samples were obtained. The soil temperature was recorded at the time of sampling. To eliminate biases, several samples from unmarked areas were also taken.

Samples were first examined visually and then subjected to Berlese-funnel extraction. This double examination ensured that various stages (particularly larvae) were not overlooked. The ticks recovered were divided by stage, sex and degree of engorgement, placed in stoppered vials containing a mixture of moist charcoal and plaster-of-Paris (Main, 1973) and stored in a refrigerated incubator at 9° ± 1°C. for later use.

Several Herring Gull (*Larus argentatus*, Pont.), Black-legged Kittiwake (*Rissa tridactyla* (L.)), *U. aalge*, *A. torda* and *F. arctica* chicks were taken from their nests soon after hatching, placed in a compartmentalized cardboard container and brought back to the laboratory for experimental purposes. The birds were kept at room temperature (24 - 30°C.) in wire or plastic rodent cages and fed fresh caplin (*Mallotus villosus*)

FIGURE 17.

Details of sampling area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9
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8
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twice daily. Two to three weeks after their capture each *L. argentatus* and *R. tridactyla* chick was eating 8 - 9 large caplin per day, each alcid chick 4 - 5 caplin per day. Domestic chickens were kept in a similar manner and fed on fish-flavoured cat food. The *L. argentatus* chicks were occasionally given this diet to conserve caplin.

Attempts were made to obtain data on certain aspects of feeding by the tick stages on the chicks. Two to three hours prior to the infestation of chicks, the ticks were removed from the incubator, left at room temperature to become active and then weighed using a Cahn Electrobalance (accuracy 0.01%). Individuals were then allowed to crawl onto the flat end of a pair of forceps and transferred to the head of a chick. The elapsed time before attachment, and the time and site of attachment were recorded. Water was placed in the bottom of the animal cages to prevent the escape of engorged specimens and to facilitate their detection. Regular checks were made on each chick and the time of dropping-off recorded. The engorged specimens were weighed, placed in vials as previously described, and stored at various temperatures. The sides of the vials were smeared with an antibiotic-antimycotic solution to inhibit fungal growth. The percentage increase in weight of all stages was calculated and molting time of larvae and nymphs recorded.

Engorged females were placed with male(s) in petri

dishes containing moist filter paper and observations made on their copulation at room temperature. The males, subsequent to copulation, were removed, and the females stored at various temperatures. The time of oviposition, the number and weights of eggs (average of 10 eggs per weighing) recorded at regular intervals.

To determine the effect of temperature and humidity on hatching, groups of 20 eggs were placed in petri dishes containing either soil or filter paper, and subjected to different temperature and humidity regimes. The eggs were checked regularly and hatching times recorded.

To investigate host (domestic chick) reaction to tick attachment, a nymphal tick plus the surrounding host tissue was removed, fixed in Bouin's fluid and sectioned (at 8 μ) using the technique outlined by Davenport (1960). The sections were stained with Harris' haematoxylin and eosin and mounted in permount.

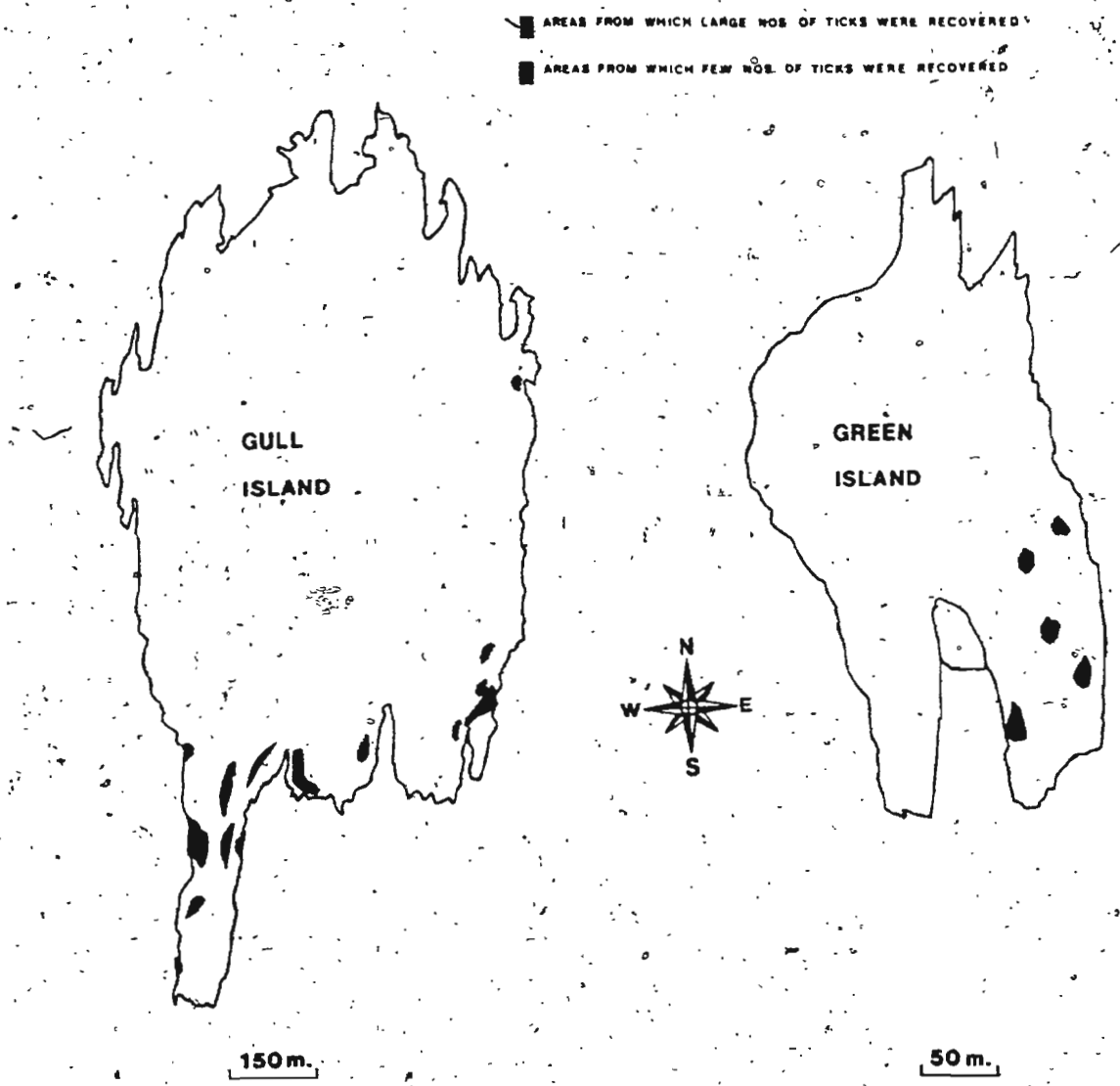
Results and Discussion

A. Distribution

All the ticks collected in the present study were from the Witless Bay Seabird Sanctuary (Fig. 18). As noted by Murray and Vestjens (1967) and Karpovich (1970) ticks were concentrated in areas where host nesting was dense although a few specimens could be found in other areas. In most of the places designated as areas of tick

FIGURE 18

Areas where ticks were recovered on Gull and Green Islands


AREAS FROM WHICH LARGE NOS OF TICKS WERE RECOVERED
AREAS FROM WHICH FEW NOS. OF TICKS WERE RECOVERED
GULL
ISLAND
GREEN
ISLAND
N
W
E
S
150 m.
50 m.

concentrations (Fig. 18) were areas of dense nesting by *F. arctica* or *U. aalge*.

The effect of host density on the distribution of *I. uriae* was again seen from samples taken from groups of marked *F. arctica* burrows (Fig. 17). The density of *F. arctica* burrows was greatest at the bottom of the slope, where some burrows were interconnecting, intermediate at the middle and sparse at the top. It was found that more ticks were recovered per sample from the burrows at the bottom of the slope (Nos. 3 to 7) with an average of 23 per individual group of burrows, than at the middle (average of 6.6 ticks per individual group of burrows) (Table 32). No ticks were recovered from the burrows sampled at the top of the slope.

Another factor affecting the distribution of *I. uriae* is the type of substrate since, as noted by Karpovich (1970), this is where metamorphosis and overwintering occur. Murray and Vestjens (1967) reported that *I. uriae* was found only in areas where the ground was sloped and well drained. In the present study, it was found that *I. uriae* occurred more frequently in loose, dry soil than in damp, heavily packed humus, regardless of the slope.

B. Seasonal Abundance

All stages (except eggs) were recovered from the soil and nest material examined. Fig. 19A illustrates the

TABLE 32.

NUMBERS OF *IXODES URIAE* RECOVERED FROM INDIVIDUAL GROUPS OF *FRATERCULA ARCTICA* BURROWS DURING 1973

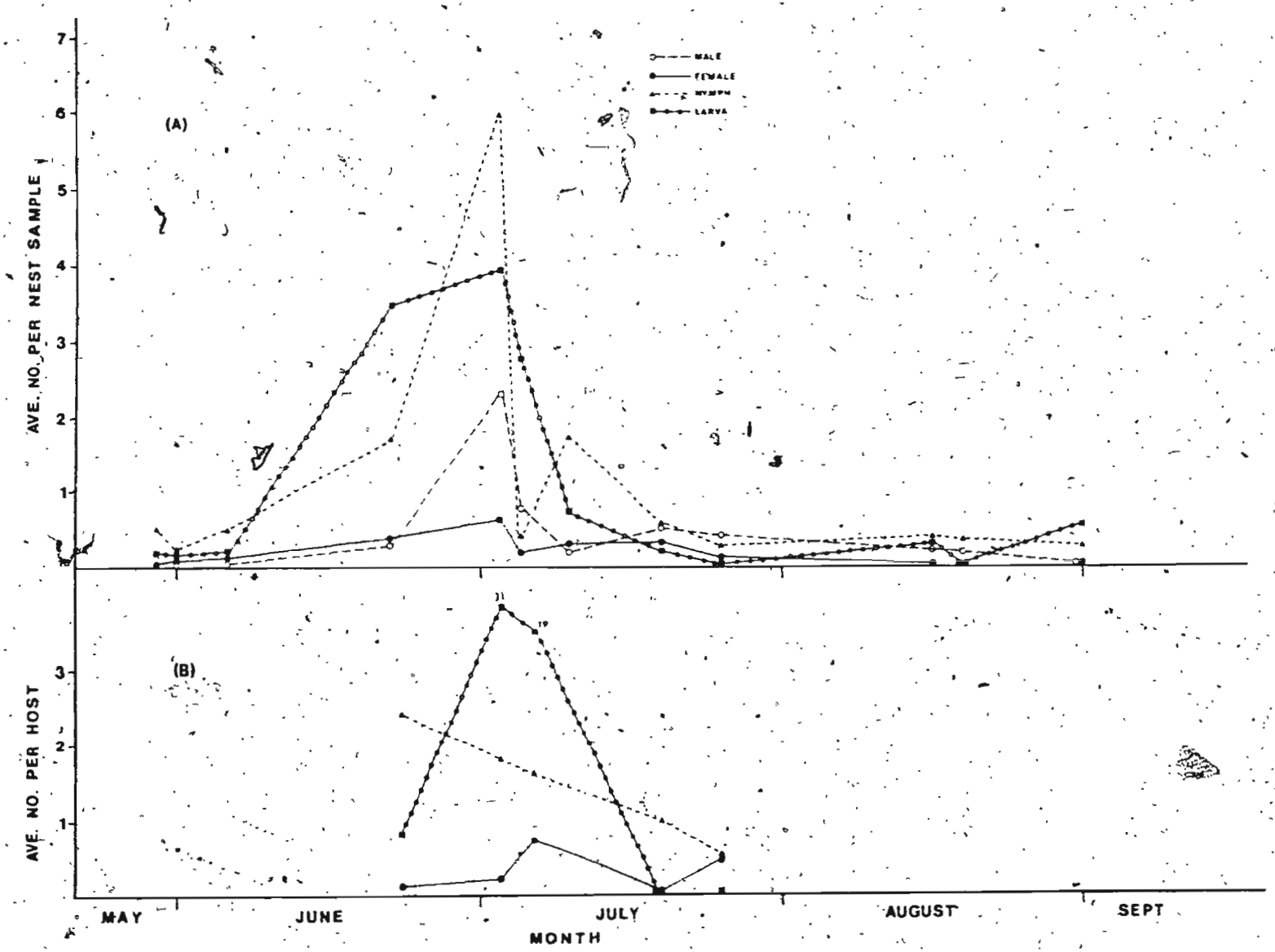
Group	Month				Total
	May	June	July	August	
1	0	0	3	1	4
2	2	1	1	3	7
3	0	19	4	0	23
4	6	41	6	3	56
5	3	7	5	0	15
6	0	11	0	0	11
7	1	1	6	2	10
8	0	1	10	0	11
9	0	1	5	0	6
10	0	4	2	0	6
11	0	8	12	0	20
12	0	4	0	0	4
13	0	1	1	0	2
14	0	1	1	1	3
15	0	1	1	1	3
16	0	0	0	0	0
17	0	0	0	0	0
18	0	0	0	0	0
19	0	0	0	0	0
20	0	0	0	0	0
Unmarked Groups	6	29	18	10	63
Total	18	130	75	21	244

FIGURE 19

The seasonal activity of *Ixodes uriae:*

A. In nesting areas

B. On hosts


(A)
AVE. NO. PER NEST SAMPLE
MALE
FEMALE
NYMPH
LARVA
(B)
AVE. NO. PER HOST
MAY
JUNE
JULY
AUGUST
SEPT
MONTH

seasonal activity of *I. uriae* collected from alcid nests. Larvae were abundant throughout June with a slight increase in activity during the last week, rising to a peak the first week of July. Engorged larvae were recovered during the last week in June and by the first week in July represented 34.4% of the total population (Table 33). All larval activity ceased about the middle of July, but became obvious again at the end of August, a time when newly molted larvae occur (Table 33). No engorged larvae were recovered after the middle of July.

Nymphs, although less abundant than larvae, exhibited similar activity in June and early July. They were the dominant stage during July although activity ceased towards the end of the month. Engorged specimens were recovered from early July to mid-August at which time newly molted nymphs were also recovered (Table 33).

Males and females showed similar activities during June, both rising to a peak early in July. During July the numbers of males dropped and remained fairly constant until the end of August. Female activity remained fairly constant during the first week of July but started to decrease towards the end of the month, none being recovered in August. Newly molted males were present in mid-August. It is interesting to note that males, previously having been reported as rare (Spencer, 1960) were more abundant (2 : 1) than females in July and August.

TABLE 33

DETAILS ON THE COLLECTIONS OF *IXODES URIAE* FROM ALCID NESTS**

Date	Unfed Female	% Unfed Female	Male	% Male	Unfed Nymphs	% Unfed Nymphs	Engorged Nymphs	% Engorged Nymphs	Unfed Larvae	% Unfed Larvae	Engorged Larvae	% Engorged Larvae	Total
5.29.73	0	0	0	0	9	75.0	0	0	3	25.0	0	0	12
5.31.73	2	33.3	0	0	2	33.3	0	0	2	33.3	0	0	6
6. 5.73	2	12.5	1	6.3	9	56.3	0	0	3	18.8	1	6.3	16
6.21.73	6	5.2	6	5.2	34	29.6	0	0	60	52.2	9	7.8	115
7. 2.73	2	5.1	7	18.0	16	41.0	2	5.1	4	10.3	8	20.5	39
7. 4.73	1	3.4	5	17.2	2	6.9	1	3.4	10	34.5	10	34.5	29
7. 9.73	5	11.9	3	7.1	26	61.9	0	0	4	9.5	4	9.5	42
7.18.73	4	16.0	9	36.0	7	28.0	2	8.0	0	0	3	12.0	25
7.24.73	1	12.5	5	62.5	1	12.5	1	12.5	0	0	0	0	8
8.15.73	0	0	4(3)*	30.8	4(1)*	30.8	1	7.7	4(2)*	30.8	0	0	13
8.18.73	0	0	1	33.3	1	33.3	1	33.3	0	0	0	0	3
8.31.73	0	0	0	0	3(2)*	33.3	0	0	6(3)*	66.6	0	0	9
Total	23	7.3	41	12.9	114	36.0	8	2.5	96	30.3	35	11.0	317

*Newly molted ticks.
**From soil samples gathered within nesting colony of A.torda, U.aalge, U.lomvia, F.arctica.

No ticks were recovered from alcids during May, early June, August and September (Fig. 19B). All parasitic stages were first recovered during the last week of June at which time nymphs were most abundant. Their (nymphs) numbers slowly decrease to a minimum by late July. Larvae were less abundant than nymphs in June but reached a peak on hosts early in July. By mid-July all larvae had disappeared from hosts. Females reached their peak abundance on hosts about the same time as larvae. Their numbers decreased to a minimum about mid-July but increased again towards the end of that month. Similar results were reported by Flint and Karpovich (1967) for *I. uriae* in Russia.

The peaks of activity for all stages occurred simultaneously in the nests and on the hosts (Fig. 19A and B). It appears that the mass occurrence of ticks at late June/early July ensures that maximum numbers of the parasitic stages will have engorged and molted before winter. The peak abundance of males (Fig. 19A) at the same time as that of females also ensures that optimum chances for mating to occur.

C. Host Preferences

In both 1972 and 1973, *U. aalge* were the preferred host of *I. uriae*, 58.3% and 50% being infested respectively. However, the average numbers per host were small, 5.1 in 1972 and 3.9 in 1973. It appears that this is a reflection of the nesting habits of *U. aalge*, being easily accessible

to ticks on the ledges.

In 1972, only 7.8% of *F. arctica* were infested with *I. uriae*, the average number per infested host being 1.8. Main (1972, unpublished data) while recording very few ticks on this host, noted that immature *L. argentatus* appeared to be the preferred host. In 1973, 29.5% of *F. arctica* were infested with an average of 19.3 ticks per infested bird. This increase could be attributed to low numbers of immature *L. argentatus* during this year due to mass mortality caused by a severe storm (Threlfall *et al.*, 1974). *Larus argentatus* chicks possess the habit of leaving their nests at a very early age and when danger threatens, secreting themselves, often in the entrance to puffin burrows in the present study area. When these chicks are 2 - 3 weeks old they will invariably manage to get only their head and anterior body region in the burrows, as a result of which ticks are frequently recovered from the heads of these birds. A similar situation was noted by Flint and Kostyrkc (1967) in Russia when *U. aalge* were scarce due to lack of food, the infestation of *R. tridactyla* greatly increased.

D. Feeding

The feeding process of the parasitic stages of *Ixodes uriae* requires many days. Table 34 details the engorgement time (days) of each stage on various hosts. Nymphs require

TABLE 34

DETAILS ON FEEDING OF *IXODES URIAE* ON VARIOUS HOSTS AT ROOM TEMPERATURE (24°-30°C.)

Host	Larvae					Nymphs					Females					% Total success
	No. used	No. engorged	% success	Feeding duration (days)		No. used	No. engorged	% success	Feeding duration (days)		No. used	No. engorged	% success	Feeding duration (days)		
				Mean	Range				Mean	Range				Mean	Range	
Razorbill (immature)	1	1	100	6.8	6.5-7	4	4	100	5	5	2	2	100	7.3	7-7.5	100
Common Murre (immature)	5	5	100	6.1	5-7	4	4	100	5.6	5-7	1	1	100	7	7	100
Common Puffin (immature)	-	-	-	-	-	-	-	-	-	-	4	3	75	7.7	7-8	75
Black-legged Kittiwake (immature)	6	0	0	-	-	7	3	42.8	6.3	4-8	3	1	33.3	8	8	25
Herring Gull (immature)	-	-	-	-	-	-	-	-	-	-	1	1	100	6	6	100
Domestic Chicken (immature)	2	0	0	-	-	7	1	14.2	6*	6	-	-	-	-	-	11.1
Total	14	6	42.9	6.3	5-7	22	12	54.5	5.6	4-8	11	8	72.7	7.3	6-8	55.3

*Died immediately after engorgement.

the least time to complete engorgement (mean 5.6 days) followed by larvae (mean 6.3 days) and females (mean 7.3 days). Balashov (1968) and Murray and Vestjens (1967) reported similar results on other hosts (Table 35), although the feeding duration of larvae and nymphs on gentoo penguins was slightly longer.

The individual differences in engorgement time of each stage on the same or different hosts may be caused by a variety of factors. The tick's physiological state may affect engorgement rapidity, Balashov (1968) reporting that not only did fewer long-unfed ticks and relatively recently-fed ticks attach than normal, but they also fed longer than normal. The same author stated that feeding was affected by tick attachment in unsuitable body areas such as those with insufficient blood supply, thick body covering, abundant grease and sweat secretions as well as pathological changes in areas with many attached ticks and host defense reactions. Balashov (1968) also reported that feeding is influenced by the season which affects both speed of attachment and feeding period in many ixodids, even in the laboratory. It is doubtful whether this would be a factor in the present study since all experiments were performed when ticks were actively feeding in the field. Experimental conditions were also the same for all feeding experiments.

It is evident from Table 34 that certain tick stages will attach and feed on certain hosts with varying success

TABLE 35

FEEDING DURATION (DAYS) OF *IXODES URIAE* REPORTED IN LITERATURE

Host	Larvae	Nymphs	Females	Source
Cormorant (*Phalacrocorax albiventer papurascens* (Lesson))	6 - 12	-	-	Murray and Vestjens (1967)
Gentoo penguin (*Pygoscelis papua* (Forster))	-	6 - 12	8	
Black Guillemot (*Cepphus grylle* (L.)) (immature)	4 - 6	4 - 8	6 - 8	Baloshov (1968)

All stages of *I. uriae* completed engorgement on *U. aalge* and *A. torda* but, in contrast, no larvae completed engorgement on *R. tridactyla*, all specimens dying *in situ* after attachment. Only 42.8% of the nymphs and 33.3% of the females that attached to *R. tridactyla* completed engorgement, one female dying *in situ* 10 days after attachment. Only one nymph of seven completed engorgement on domestic chickens, but it died immediately after dropping-off. Other workers (Nuttall, 1913; Flint and Kostyrke, 1967) have reported similar results in feeding experiments with *I. uriae* using non-seabird hosts.

Arthur (1965) reported that *Ornithodoros moubata* will not grow by feeding on rats showing the thiamine deficiency, and it may well be that *Ixodes uriae's* failure to complete development on non-seabird hosts could be due to the lack of certain substances in the blood of these hosts. The diet of the host appears to have no effect since the domestic chickens were fed the same type of food as the experimental alcids. At the present time no explanation can be offered to explain this failure to develop on certain hosts.

The feeding sites of the various stages of *I. uriae* on hosts in the laboratory are shown in Table 36. As mentioned earlier, the preferred sites for the stages, except females, on hosts in the field were the breast and back regions. In contrast, all stages preferred the head of the hosts in the

TABLE 36

FEEDING SITES OF THE STAGES OF *IXODES URIAE* ON VARIOUS HOSTS IN THE LABORATORY*

Tick Stage	Head					Other Areas		
	Eyelid		Angle of Mouth	Crown	Gular	Neck	Breast	Web of Foot
	Right	Left						
Larva	2	1	1	1	1	-	-	-
Nymph	4	3	2	1	1	-	1	-
Female	1	1	-	3	1	1	-	1
Subtotal	7	5	3	5	3	1	1	1
Total	23					3		

*Ticks initially placed on head of host.

laboratory. This may be due to the ticks being initially placed on the head of the hosts but the fact that little wandering by the ticks occurred in selecting a feeding site is significant. Most of the ticks localized around the eyes of the hosts, a position noted by Karpovich (1970) for many ticks on *U. aalge*.

While it may be speculated that engorged specimens of *I. uriae* exhibit a distinct detaching rhythm in the field to ensure that the site is favourable for further development, this phenomenon was observed in the laboratory. The majority of engorged specimens (69.2%) detached from their hosts at night. Furthermore, all the specimens which attached to an *A. torda* chick in the field, detached during the night in the laboratory. In the field, the night time is the period when birds are on their nests and relatively inactive. The fact that this rhythm was still expressed in the laboratory is remarkable when one considers that the hosts are almost continually inactive and the photoperiod is rather inconsistant. This nocturnal detachment rhythm has been reported for a variety of ticks (Balashov, 1968; Arthur, 1962) and is undoubtedly an inherent survival mechanism.

Although many studies have been done on the attachment and feeding of ticks, none have been done on *Ixodes uriae*. Histopathological changes in the skin of a domestic chicken were studied 48 hours (approximately one-third of the total

feeding time) after attachment. By this time the mouthparts were fully inserted into the skin; the hypostome (h) within the epidermis and the chelicerae lying parallel with the digits (d) flexed laterally (Fig. 20A). The depth of penetration was approximately 135 μ but it is not known whether all stages penetrate the skin to a similar extent. Moorhouse and Tatchell (1966) reported that despite the great difference in size of the mouthparts of the stages of *Boophilus microplus* and the time since attachment, the depth of penetration was almost identical and not a function of their length as suggested by Arthur (1965).

The cement layer (c.l.) Figs. 20A and B) is deposited internally around the mouthparts as noted for *Ixodes ricinus* (Arthur, 1962). This layer ensures that the tick is not dislodged by the host when preening and, in fact, anchors the tick so firmly that forcible removal of an attached tick, often results in leaving the mouthparts *in situ*. As noted by Moorhouse and Tatchell (1966) for *Boophilus microplus*, a layer of secondary cement (s.c.l.) appears to have been deposited around the tip of the hypostome and cheliceral digits (Fig. 20A) to compensate for the loss of support generated by a swelling of the skin after the initial phase of engorgement. The palps (p) remain closely applied to the outer surface of the skin (Fig. 20A).

Around the hypostome are areas of edema, necrosis, leucocyte infiltration, cavitation, and vasodilation. In section (Fig. 20A), these are arranged concentrically with

FIGURE 20

Histopathological changes in the skin of a domestic chicken, 48 hrs. after *Ixodes uriae* attachment.

A. Section of skin and mouthparts of *I. uriae*.

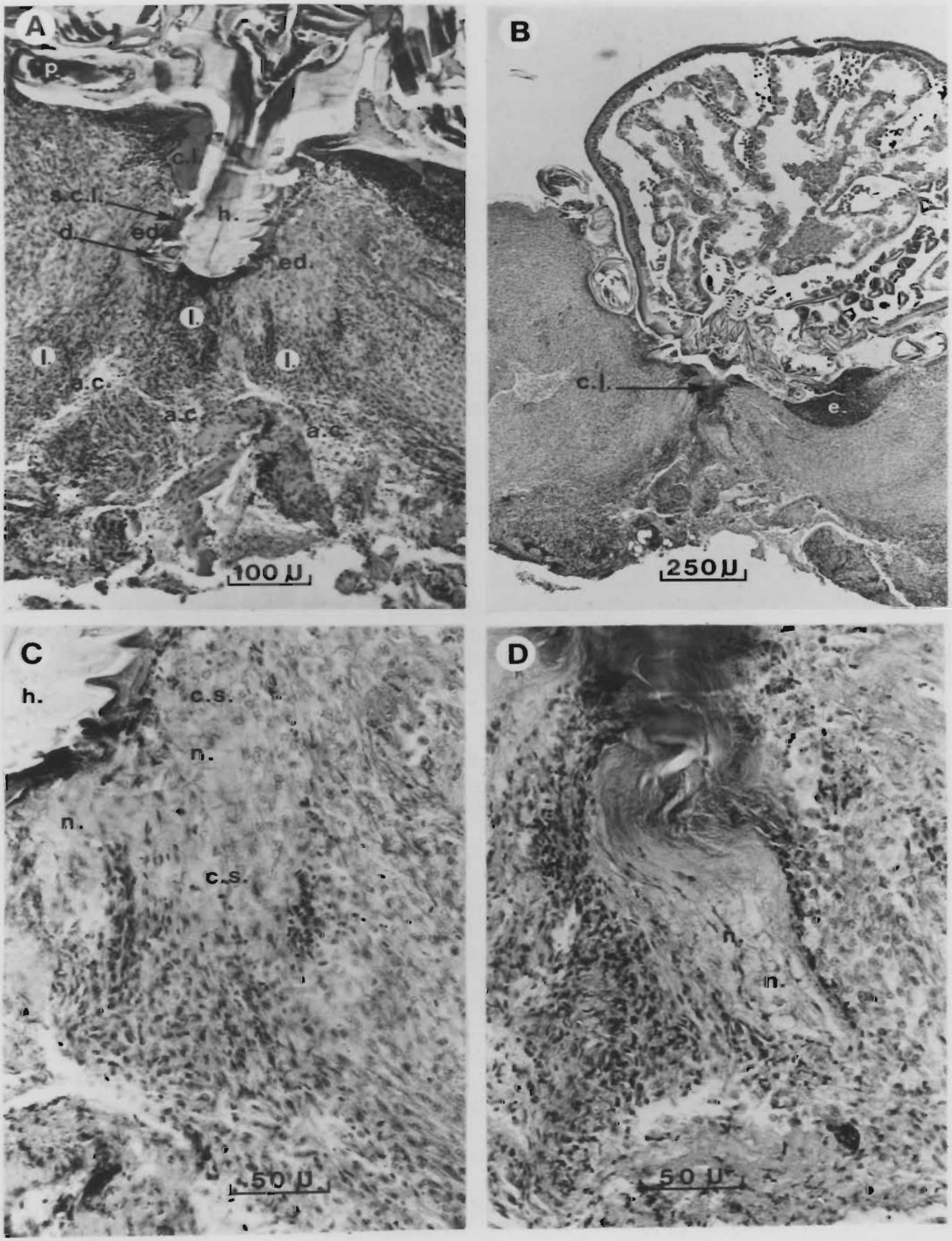
B. Section of skin and tick showing extent of reaction to attachment.

C. Section of skin adjacent to hypostome showing areas of necrosis and cloudy swelling.

D. Necrotic-edematous area near tip of cement layer.

Abbreviations

a.c. area of cavitation
c.l. cement layer
c.s. cloudy swelling
d. cheliceral digit
e. eosinophilic reaction
ed. edematous tissue
h. hypostome
l. leucocyte infiltration
n. necrotic area
p. palp
s.c.l. secondary cement layer.


A
p.
c.l.
s.c.l.
h.
d.
ed.
ed.
l.
l.
l.
a.c.
a.c.
a.c.
100 µ
B
c.l.
e.
250 µ
C
h.
c.s.
n.
n.
c.s.
50 µ
D
n.
n.
50 µ

the hypostome as the centre.

Edematous tissue, (ed.) produced by salivary secretions (Arthur, 1965), were observed immediately distal to the hypostome (Fig. 20A). This interstitial fluid may contribute to the diet of the tick (Arthur, 1965). Lighter colored gut contents were observed in certain larvae and nymphs undoubtedly caused by the ingestion of this fluid (Arthur, 1965). Areas of cloudy swelling (c.s.) and necrotic tissue occurred near the tip of the hypostome (Figs. 20C and D). Similar results were reported by Arthur (1951) for *Ixodes hexagonus*.

A leucocyte infiltration of predominantly lymphocytes and eosinophils (l) occurred next to the necrotic-edematous area (Fig. 20A), a similar situation being observed in the feeding of adult female *Boophilus microplus* (Tatchell and Moorhouse, 1968). Adjacent to this infiltration were areas of cavitation (a.c.) (Fig. 20A). In the area of the primary cement layer, a number of arteries were dilated and had perivascular lymphocyte infiltration (p.l.) (Figs. 21A and B).

Tatchell and Moorhouse (1968) reported that there was a tendency for eosinophils to increase during feeding of *Boophilus microplus*. These eosinophils form a denser aggregation towards the periphery of the area of intense infiltration. Larrivee (1964) noted that an increased eosinophilia is characteristic of immediate or anaphylactic

FIGURE 21

Histopathological changes in the skin of a domestic chicken 48 hrs. after *Ixodes uriae* attachment.

A. Area of vasodilation.

B. Perivascular lymphocyte infiltration near cement layer.

C. Eosinophilic reaction near palp and leg.

D. Section of damaged skin near hypostome.

E. Section of normal skin.

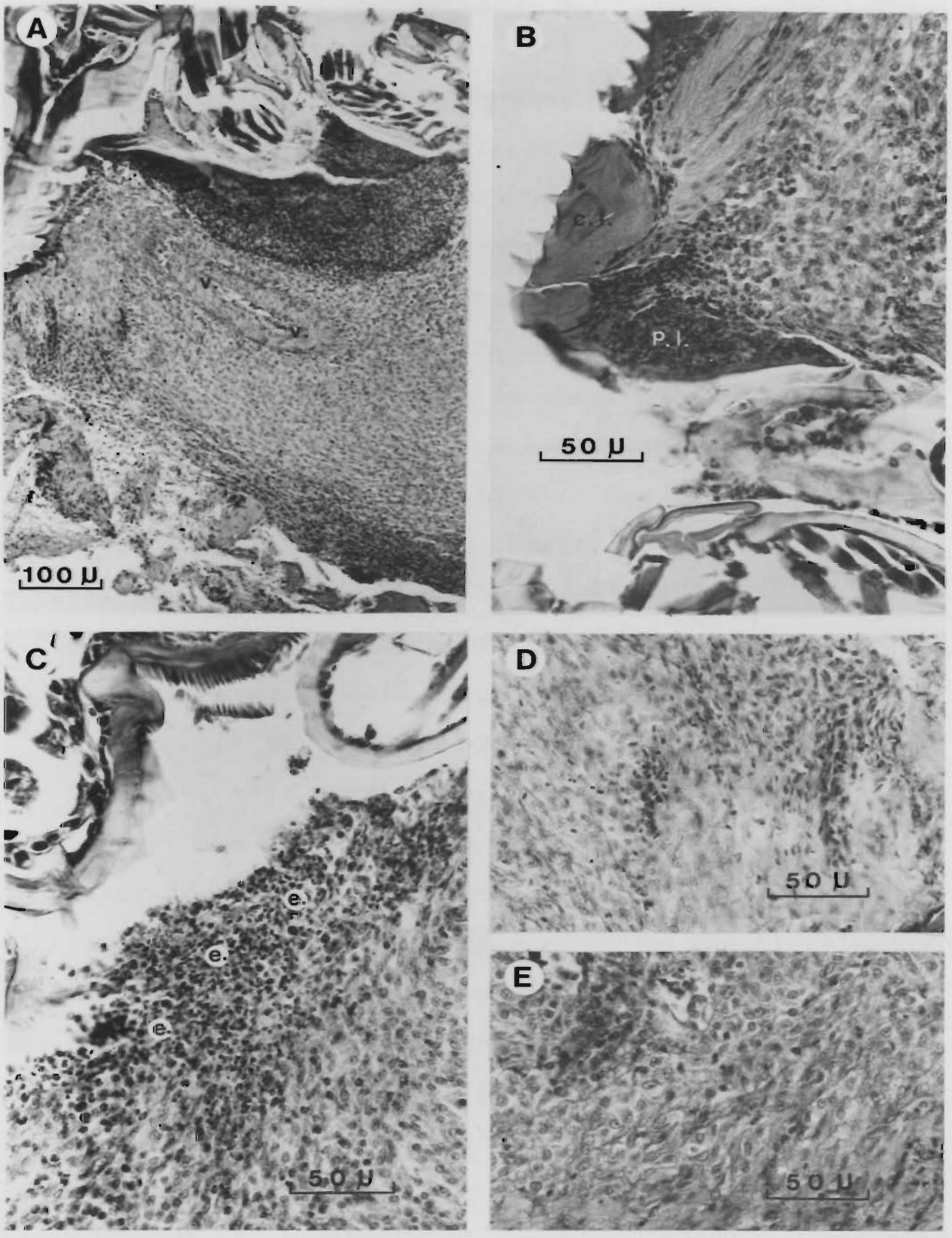
Abbreviations

c.l. cement layer

e. eosinophilic reaction

p.l. perivascular lymphocyte infiltration

v. vasodilation.


A
v
v
100 µ
B
P. I.
50 µ
C
e.
e.
e.
5.0 µ
D
50 µ
E
50 µ

response to bites of haematophagous arthropods. There was eosinophilic (e) reaction in the area around a palp and legs of the tick (Fig. 20B). Whether the palps and legs mechanically damage the skin through movements when feeding is not known but seems probable since in the area of the legs the epithelium was also missing (Fig. 21C).

From Fig. 20B it is evident that there was an intense localized reaction to the attachment of *I. uriae*, over one-half of the tick being engulfed in the host's skin after just one-third of the normal attachment time. Undoubtedly this partial encystment of the tick is due to the inflammatory swelling of the skin causing it to rise above the subjacent tissue in which the hypostome is buried (Arthur, 1962). A comparison of skin near the hypostome (Fig. 21D) to "normal" skin (Fig. 21E) shows the extent of the host response to the tick bite.

Since the host studied may be regarded as "unnatural", the extent of the host reaction may be different than that of a "natural" host. Hoeppli and Schaumacher (1962, *vide* Tatchell and Moorhouse, 1968) in a study on the histological reactions to trombiculid mites on "natural" and "unnatural" hosts, failed to find any constant correlation between host type and the type or intensity of reaction. Tatchell and Moorhouse (1968) likewise reported that significant differences were found only in the eosinophil infiltration for a short period of attachment of *Boophilus microplus* and also

in the Zebu cattle type lesions associated with larvae from the second to the fourth day. Dineen (1963) demonstrated that "natural" hosts produced fewer antibodies to parasites than did "unnatural" hosts, thus suggesting that "natural" hosts respond less vigorously. Tatchell and Moorhouse (1968) noted that the less adapted host is rendered more susceptible since it becomes sensitized and a more severe local response occurs which results, for the parasite, in a more ready access to tissue fluids. As previously mentioned, *I. uriae* would rarely complete engorgement on domestic chickens (Table 34), and if successful, died immediately upon detachment. The extensive host response seen in the present study may, in some way, be a contributing factor to this failure.

Weight increases in the parasitic stages of *I. uriae* during feeding are given in Table 37. The larval stage of *I. uriae*, in both the unfed and engorged states, is heavy when compared to the weight of this stage of other tick species reported by Balashov (1968). However, its weight increased only 12.4 times after engorgement which is low on the range (10 - 20 times) reported for larvae of other species, but is similar to that reported for *Ixodes ricinus* (12.4 times). The unfed nymphal stage of *I. uriae* is likewise heavy in comparison to other tick species, but the increase in weight (26 times) after engorgement is rather low, falling in the range (20 - 30 times) reported for

TABLE 37

INCREASE IN BODY WEIGHT (MG.) OF THE PARASITIC STAGES OF *IXODES URIAE* DURING FEEDING

Weight (mg.)	Larvae		Nymphs		Females	
	Mean	Range	Mean	Range	Mean	Range
Unfed	0.0568	0.0420-0.0725	0.3990	0.3470-0.4220	5.565	4.910-6.673
Completely Engorged	0.6919	0.502 -0.8595	10.213	7.008-12.564	138.0	87.1-177.7
Percent Increase	1242	850-1583	2607	1754-3263	2475	1448-2892

Ixodes ricinus, *Haemaphysalis punctata* and *H. sulcata* reported by Balashov (1968). In comparison with the reported unfed weights of female of other species, *I. uriae* is intermediate, but the engorged weight is low, closely corresponding to that reported for *Ixodes laguri laguri* (Shevchenko, 1956; *vide* Balashov, 1968). The average weight increase is also small (24.8 times) in comparison with increases reported for other species (80 - 120 times). Balashov (1968) reported similar results for females of *I. uriae*, noting that weight increases in burrow-parasitic ixodids is much less than in field-parasitic species.

The average weight of 10 males was 7.839 mg., this being approximately 2 mg. more than the average weight of females. Nuttall (1913) reported that larger nymphs molted into males, arguing that males have to store up more energy for its sexual life. In view of the fact that males do not feed, its larger weight could be attributed to its mode of life.

E. Observations on Reproduction

Very few observations have been made on ixodid copulation; none on *Ixodes uriae*. In the present study, the mating behavior of engorged females and males of *I. uriae* was observed in glass petri dishes, the bottom of which was covered with moist filter paper. It appears that

males "recognize" females by contact since no interest was expressed in the female until contact occurred. The male then crawled over the body of the female in a posterior direction, seeking to get beneath her. This was achieved by climbing beneath the female from the posterior end as was described for *Ixodes trianguliceps* (Arthur, 1962). The female keeps crawling about, apparently ignoring the efforts of the male. The male advances towards the anterior of the female, and comes to rest with its first pair of legs clinging to the trochanter of the first pair of legs of the female so that they are visible from the dorsal side of the female. For approximately 10 minutes after crawling under the female, the males other pairs of legs were constantly moving over the sides of the female finally coming to rest with the second pair of legs around the third pair of the female and the third pair around the fourth pair of the female. The male's fourth pair of legs rested upon the sides of the female. The female remained motionless at this point, her movements being restricted by the males position. The male's chelicerae and hypostome were inserted into the female genital opening with the palps deflected to the sides. Contrary to that reported by Arthur (1962) for other *Ixodes* species, attachment is not only maintained by the mouthparts, but the legs as well.

Details on the exact method of transfer of the spermatophore to the female genital opening by the male

mouthparts are not available. However, before the spermatophore was placed into the female opening, the area around it was protuberant, afterwards it became very depressed with only the bulb of the spermatophore visible on the ventral surface of the female. It is evident that the neck of the spermatophore is drawn into the female vagina by this action. The male then left its position beneath the female from the side, crawling out between the legs. The males died within 6 - 12 hours after completion of copulation at room temperature. The average completion time of 4 matings was 24.9 hrs. (range 18.5 - 31).

To determine whether an engorged female would mate more than once, an unmated male was placed in a petri dish with a mated female. Copulation commenced, lasting for just 12 hours. It is not known whether the second mating is shorter than usual. It also appears that males will mate a second time, at least with the same female since one male was observed to mate again with the same female soon after the initial mating. A second spermatophore was placed into the female opening just 2 hours after the male attained his position under the female.

From laboratory observations on mating, it appears that, in nature, it occurs by the chance meeting of the sexes. However, males must actively seek females to ensure their fertilization. In the laboratory it was found that if several unmated males were placed in a dish with an

unmated female, they all tried to mate at once with some males mounting the male already *in copulo*. Rothschild and Clay (1961) reported *I. uriae* mating beneath stones with four or five males standing by waiting their turn. No observations were made to determine whether males would mate with unfed females.

A spermatophore was recovered from a male just prior to its insertion into the female genital opening. Measurements of the spermatophore, compared with those of Nuttall, 1913 (in parentheses) were as follows: total length 2090 (1.1 mm.); bulb length 520 (0.3 mm.); bulb width 426 (0.3 mm.); neck length 1570 (-); neck width 166 (0.1 mm.).

F. Oviposition

Engorged, fertilized females were kept on moist filter paper in petri dishes and stored at 7° ± 1°C. and 9° ± 1°C. (constant darkness). One female kept at 7°C. commenced ovipositing on the 75th day after fertilization, laying all its eggs by the 110th day. Similar results were reported by Murray and Vestijens (1967) for a newly engorged female under similar conditions. In contrast, a female kept at 9°C. commenced ovipositing on the 56th day after fertilization, the whole process being completed in approximately 85 days, (the exact time was not determined due to malicious tampering with the controlled environment chambers).

Laboratory observations by Flint and Kostyrkc (1967) showed that at 20°C. oviposition occurred after 7 - 14 days but at 15°C. only after 14 - 22 days.

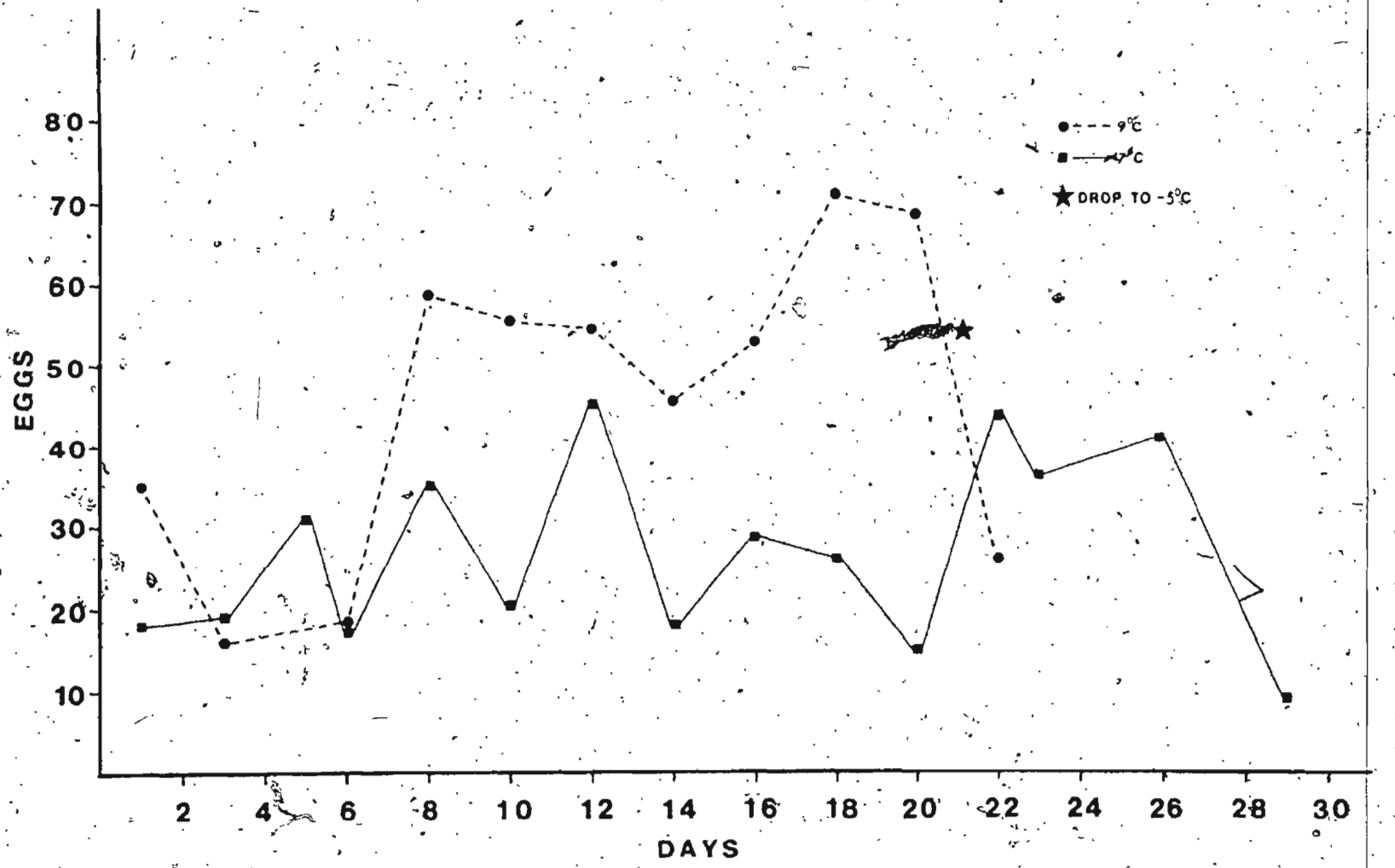
It is quite obvious that the length of oviposition is directly dependent on the temperature. In the field where the average soil temperature is 9.4°C., oviposition is a lengthy process. Comparisons cannot be accurately made with the data of other workers since most observations were reported from females of unknown ages.

The total number of eggs deposited by a single female ranged from 522 - 554, the number of eggs laid daily varying from 4 - 35. This number is considerably higher than that reported by other workers (12 - 380 eggs, Nuttall, 1913; 251 - 359 eggs, Flint and Kostyrkc, 1967; 193 - 425 eggs, Murray and Vestjens, 1967).

The egg production by females of *I. uriae* at different temperatures (constant darkness) is illustrated in Fig. 22. It was found that the overall diurnal productivity was higher at 9°C. Between days 20 and 22, a severe temperature drop to -5°C. in the 9°C. environment caused a severe drop in the egg production, a further indication of the serious effect of temperature on oviposition. The erratic egg laying by the females under both environmental conditions does not allow one to draw definite conclusions about peaks of egg laying although it appears that 2 peaks may occur; one between days 8 - 12 and the other between days 18 - 22

FIGURE 22

Egg production of *Ixodes uriae* at 9°C and 7°C (constant darkness).


80
70
60
50
40
30
20
10
EGGS
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
DAYS
9°C
DROP TO -5°C

depending on the temperature. Peaks of egg laying have been reported in other species (Arthur, 1962). Groups of 10 eggs, as laid by a female kept at 9°C, were weighed throughout the course of egg laying. The average egg weight on the first day of egg laying was 0.060 mg. This gradually increased, reaching a peak of 0.078 mg. by the 11th day after which time the weight slowly decreased (0.072 on day 15 and 0.071 on day 17). Although no eggs were weighed after this time due to changes in temperature as previously noted, it appears that the weight would have remained relatively constant or decreased very slowly until the termination of the egg laying period. Similar results were reported by Kitaoka and Yajima (1958) for *Boophilus microplus* Canestrini.

G. Development

Eggs of known age were placed on moist or dry filter paper or soil and subjected to various temperature regimes. At 3 - 4°C. (approximately fall temperature in field) 8 eggs (8%) hatched in 157 - 196 days, while at 9°C., only 2 eggs (2%) hatched in 181 days. Eggs kept at the above temperatures are still viable at the time of writing; approximately 13 months after oviposition. Interestingly, eggs only hatched under moist conditions, all those under dry conditions desiccating within 1 - 2 weeks. Murray and Vestjens (1967) reported that eggs hatched in dry to moist conditions but

not submerged in water. Nuttall (1913) reported that eggs at 12°C., hatched in 84 - 129 days.

The entire developmental process from fertilization of the female to the hatching of the egg is completed within 242 - 306 days (3 - 9°C.) in the laboratory. Similar results were reported by Flint and Kostyrko (1967).

In the laboratory, 4 completely engorged larvae molted into nymphs in 79 - 105 days at 9°C. In contrast, 7 partially engorged nymphs which were removed from a host before repletion, molted into nymphs in 80 days at 9°C. Although it is known that a certain blood volume must be imbibed before molting will occur (Balashov, 1968), it is not known whether the extent of engorgement influences the duration of the molt. Murray and Vestjens (1967) reported that 2 engorged larvae molted in 73 and 93 days, while Flint and Kostyrko (1967) noted that the molting period of engorged larvae was 50 days. Since the temperatures were not reported in the above studies, adequate comparisons cannot be made. Likewise, comparisons with the data of Nuttall (1913) would be meaningless since the data is for engorged larvae of unknown ages.

Five engorged nymphs molted into adult males and females in 71 - 145 days at 9°C (constant darkness). Murray and Vestjens (1967) reported that engorged nymphs molted into adults in 61 - 101 days (no data on temperature), while

Flint and Kostyrko (1967) reported the nymphal developmental period to be an average of 55 days (no data on temperature). It is interesting to note that 4 of the 5 engorged nymphs molted into males. Fig. 23 shows a newly molted female with cast cuticle.

In sum, the whole life cycle of *Ixodes uriae* can be completed in the laboratory in 407 - 579 days (including feeding duration for all stages). These results are somewhat higher than those reported by Murray and Vestjens (1967) but as these workers reported data from stages of unknown age held at different temperatures no valid comparisons can be drawn.

H. Life-cycle.

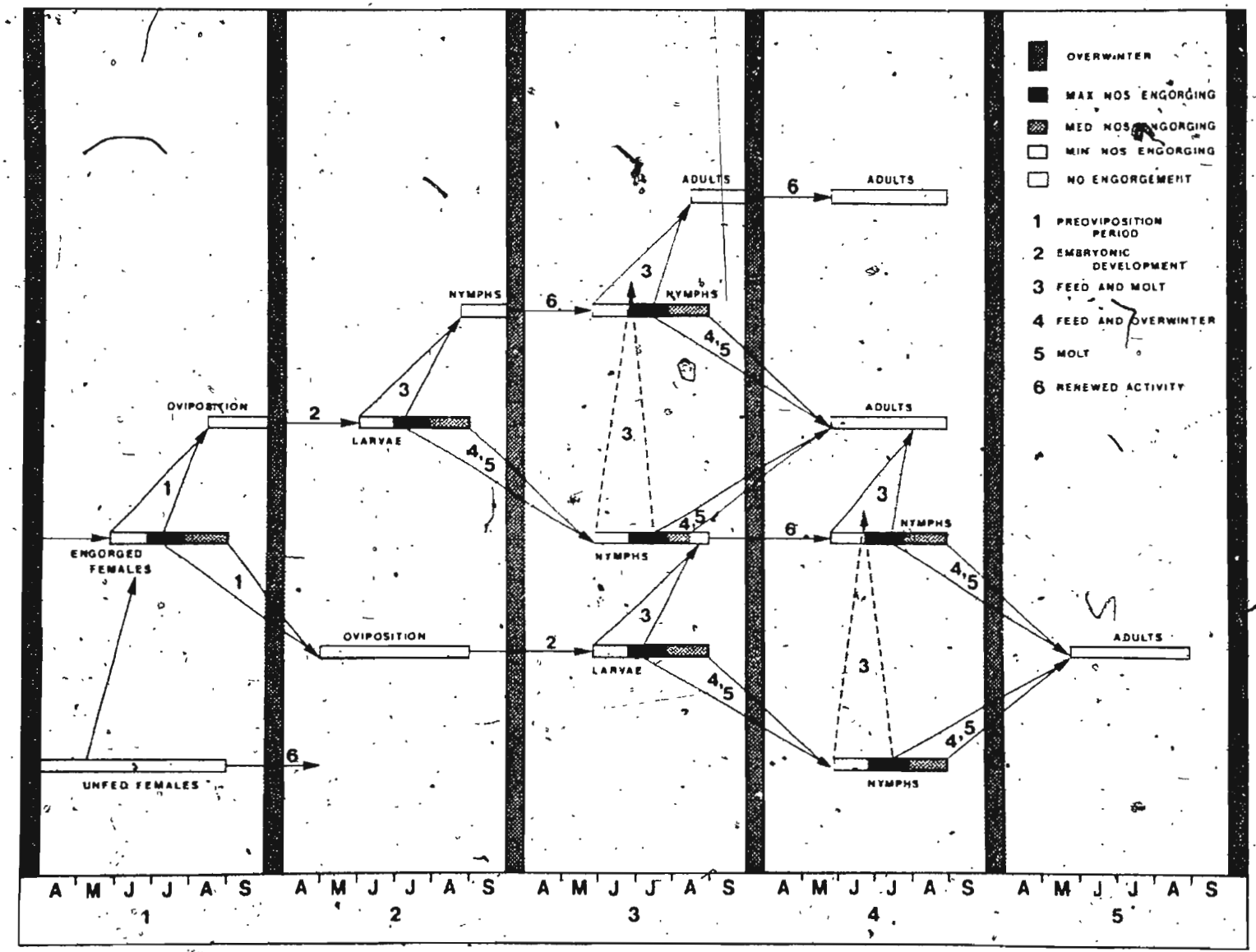
The life-cycle of *Ixodes uriae* in Newfoundland, based upon field and laboratory data, is illustrated in Fig. 24. Unfed adults may feed on seabirds from late May to late August, with maximum engorging in late June and early July. Females that have engorged before the first week of July will oviposit during that year, the eggs overwintering with larvae emerging about the end of May and the first of June of the following year. Females that engorged after mid-July will overwinter in the engorged state, ovipositing early in the following year. A few of the larvae that emerged in the 2nd year will feed and molt into nymphs that year; the nymphs overwintering in the unfed state. The majority of

FIGURE 23

Newly molted *Ixodes uriae* female with cast cuticle.

FIGURE 24

The life-cycle of *Ixodes uriae* in Newfoundland


OVERWINTER
MAX NOS ENGORGING
MED NOS ENGORGING
MIN NOS ENGORGING
NO ENGORGEMENT
1 PREOVIPOSITION PERIOD
2 EMBRYONIC DEVELOPMENT
3 FEED AND MOLT
4 FEED AND OVERWINTER
5 MOLT
6 RENEWED ACTIVITY
ADULTS
NYMPHS
LARVAE
OVIPOSITION
ENGORGED FEMALES
UNFED FEMALES
A M J J A S
1
2
3
4
5

larvae will feed and overwinter, molting into nymphs the following year. In the 3rd year, the overwintering nymphs will become active and feed, the nymphs engorging before mid-July molting to become adults which overwinter in the unfed state. Larvae that overwintered in the engorged state molt into nymphs in late May and early June. The few nymphs which feed prior to mid-July will molt into adults that year; the adults overwintering in the unfed state. The majority of nymphs which emerged that year, will feed after mid-July and overwinter in that state, the adults emerging the next year. A few of the larvae which emerged early in the year will feed and molt into nymphs that year, while the majority will feed and overwinter in the engorged state. These newly molted nymphs will overwinter in the unfed state. In the spring of the 4th year, adults which overwintered in the unfed stage become active and nymphs which overwintered in the engorged state molt into adults. The nymphs which overwintered in the unfed state become active, those feeding before mid-July molting into adults, the others overwintering in the engorged state and molting into adults early in the 5th year. Larvae which overwintered in the engorged state molt into nymphs, a few of which feed and molt into adults that year, while the majority feed and overwinter in the engorged state, molting into adults in the spring of the 5th year. Thus, depending upon the microclimate and the availability

of hosts, the life-cycle can be completed in 4 - 5 years, with the majority of the population having a 4 year life cycle.

Flint and Kostyrko (1967) likewise reported the life-cycle of *I. uriae* to be 4 - 5 years although the duration and occurrence of certain stages during similar periods of time differed from those reported above. The genetic isolation of *I. uriae* in Russia and Newfoundland may well account for this discrepancy in results.

Summary

1. The distribution of *Ixodes uriae* depended upon the density of the nesting birds and the type of substrate.

2. All stages (except eggs) showed similar peaks of activity in the nests with maximum activity occurring the last week of June and the first week of July. Newly molted males, nymphs and larvae were recovered in August.

3. *Uria aalge* was the preferred host of *I. uriae*. *F. arctica* was more heavily infested in 1973 than 1972 due to the reduction in numbers of immature *L. argentatus* as hosts at that time.

4. The engorgement times for each stage show that nymphs require the least amount of time to engorge, followed by larvae and females. The percent feeding success on various hosts indicate that *U. aalge* and *A. torda* allow all stages to successfully complete engorgement, while others

permit little success.

5. The feeding sites of all the stages in the laboratory indicate that, when placed on the head of a host, they prefer this area despite their preference for other areas on hosts in the field.

6. Within 48 hours after attachment to a host, it was found that the cement layer had been secreted and feeding had commenced. The pathological reaction of the host's skin was described.

7. Percentage weight increases of each stage after engorgement indicate that larval weight increases less, followed by females and nymphs. Males were heavier than females and eggs heavier than larvae.

8. Observations on reproduction indicate mating is a long process, extending for an average of 24.9 hours. Mated females would mate again with an unmated male and a previous mate, in both cases the mating being shorter. In nature, it appears that mating occurs by chance meeting of the sexes. Measurements of a spermatophore are given.

9. Oviposition commenced on the 75th day after fertilization at 7°C. and on the 56th day at 9°C. The rate of egg production depended upon the temperature, being higher at higher temperatures. Eggs laid on the first day of oviposition weighed less than those laid on the 11th day, after which time egg weight slowly decreased. An average of 533 eggs were laid per female.

10. Eggs hatched in 157 - 196 days at 3 - 4°C. and in 181 days at 9°C. under moist conditions, the entire developmental process from fertilization to hatching lasting 242 - 306 days (3 - 9°C.). Larvae molted into nymphs in 79 - 105 days at 9°C., while nymphs molted into adults in 71 - 145 days (9°C.). The life-cycle can be completed in the laboratory in 407 - 579 days (including feeding duration). In the field, the life-cycle requires 4 - 5 years.

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APPENDIX 1

BODY WEIGHT (GM.) AND MALLOPHAGA INFESTATION (UNITS) OF *URIA LOMVIA*

Body Weight	Mallophaga Infestation	Body Weight	Mallophaga Infestation
593	7	832	0
609	3	835	40
645	53	840	8
650	26	840	4
667	16	852	1
673	64	869	2
683	26	872	1
712	18	877	6
712	49	886	1
712	1	887	64
727	45	909	1
728	12	912	5
729	20	922	3
739	38	935	4
748	51	957	0
756	33	958	0
759	21	966	6
774	13	966	4
782	3	972	3
792	55	979	0
795	0	989	1
797	2	1017	5
803	76	1018	0
813	3	1034	2
816	0		
830	6		
831	6		